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Quantitative Comparison of Plant Community Hydrology Using Large-Extent, Long-Term Data

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ABSTRACT

Large-extent vegetation datasets that co-occur with long-term hydrology data provide new ways to develop biologically meaningful hydrologic variables and to determine plant community responses to hydrology. We analyzed the suitability of different hydrological variables to predict vegetation in two water conservation areas (WCAs) in the Florida Everglades, USA, and developed metrics to define realized hydrologic optima and tolerances. Using vegetation data spatially co-located with long-term hydrological records, we evaluated 7 variables describing water depth, hydroperiod length, and number of wet/dry events; each variable was tested for 2-, 4- and 10-year intervals for Julian annual averages and environmentally-defined hydrologic intervals. Maximum length and maximum water depth during the wet period calculated for environmentally-defined hydrologic intervals over a 4-year period were the best predictors of vegetation type. Proportional abundance of vegetation types along hydrological gradients indicated that communities had different realized optima and tolerances across WCAs. Although in both WCAs, the trees/shrubs class was on the drier/shallower end of hydrological gradients, while slough communities occupied the wetter/deeper end, the distribution of *Cladium*, *Typha*, wet prairie and *Salix* communities, which were intermediate for most hydrological variables, varied in proportional abundance along hydrologic gradients between WCAs, indicating that realized optima and tolerances are context-dependent.

KEYWORDS

conditional density estimates, EDEN, Everglades, hydrological gradients, hydroperiod, random forest classifier, realized optima and tolerances, water depth, wetland vegetation

INTRODUCTION

Although wetlands are crucial to general ecosystem health, over 50% have been lost globally (Barbier et al 1997; Mitsch and Gosselink 2007), making wetland restoration a pressing environmental priority. A major driver of wetland vegetation distribution and community dynamics is the hydrologic regime (Ross et al 2003; Ogden et al 2005; Mitsch and Gosselink 2007; Larsen et al 2011; McVoy et al 2011). Hydrologic tolerances and optima for wetland plant species are typically defined by laboratory, mesocosm or field experiments in which individual plants are grown under controlled water depths and hydroperiods (Grace 1989; David 1996; Newman et al 1996; Edwards et al 2003; Busch et al 2004; Jones et al 2006; Macek et al 2006; Deegan et al 2007; Spalding and Hester 2007). These studies, however, can provide information for only a limited number of species and can rarely be extrapolated to more complex natural settings, where species interactions and other environmental factors influence community composition.

In contrast to species' hydrologic tolerances, definitions of plant community hydrologic regimes historically have been descriptive rather than experimental. These studies have been based primarily on observations of community presence in the field and association of this presence with hydrology, either inferred or measured from a small number of samples that do not represent the full range or distribution of conditions across a landscape (Loveless 1959;

Gunderson 1994; White 1994; McVoy et al 2011). Over the past several decades, however, technological advances in environmental monitoring have allowed us to build longer hydrological records over larger spatial extents. For example, the Everglades Depth Estimation Network (EDEN) provides a network of water gages spread across the southern Florida Everglades that allows for interpolated daily water surface estimates; when coupled with a relatively dense set of systematic elevation samples, it becomes possible to estimate water depth across large spatial extents (Desmond and Survey 2007; Jones and Price 2007; Pearlstine et al 2007; Palaseanu and Pearlstine 2008; Liu et al 2009; Xie et al 2011). EDEN estimates hydrologic data daily for 42,415 400 x 400 m grid cells covering a total area of 678,640 ha, and the data archive goes back to 2000. Combining such hydrologic datasets with landscape-level community information, we now can quantify *in situ* hydrologic regimes of plant communities across large spatial extents. This quantification is important, as wetland restoration targets often associate restoration of a particular community with restoration of a particular hydrologic regime (McVoy et al 2011; LoGalbo et al 2013), but this association is not based on quantification of the full range of biotic and abiotic conditions in the landscape. Having large-extent datasets that cover different landscape units allows analysis of vegetation/hydrology relations of sub-regions that differ in hydrology or hydrological management.

Datasets with high temporal resolution and long temporal extent also provide the opportunity to construct hydrologic variables that may have greater biological meaning than traditional metrics such as mean annual water depth. Hydrology can be quantified in a number of ways; variables often include measures of depth and duration of wetness (hydroperiod), as well as flow rate. Typically, variables such as annual mean water depth or hydroperiod length are defined based on Julian years (January 1 to December 31), and data are summarized as averages across years (David 1996; Givnish et al 2008; Todd et al 2010). In seasonal wetland environments, however, such measures smooth out variations that may be important in defining differences among plant community types. For example, some environments dry out annually for a short time, whereas others dry out only every several years but for longer periods. These two environments could have very similar average hydroperiods, but very different types of vegetation based on the different periodicities of wetness.

In this study, we analyzed vegetation/hydrology associations for different wetland communities across two Everglades water conservation areas (WCAs). We used vegetation data collected with the EDEN elevation samples to create a large-extent, long-term hydrology dataset for the vegetation point locations. Our first goal was to select different types of hydrological variables to interpret the presence of diverse wetland plant communities. The variable selection process was based on accuracy of vegetation prediction from different sets of variables defining water depth, hydroperiod, and wet dry/events for different temporal extents and different definitions of temporal units. Our second goal was to define realized plant community hydrologic optima and tolerances for the variables selected. To accomplish this, we used the vegetation data set in conjunction with the large extent hydrology dataset that had high spatial resolution to develop abundance-based density estimates and conditional probabilities for plant communities along gradients of the selected hydrological variables within each WCA, and we evaluated whether these variables differed by vegetation type.

MATERIALS AND METHODS

Study Area and Data Sources: To evaluate the relationship of hydrological variables to wetland vegetation patterns, we used spatially-explicit, coincident hydrological records and plant community data for two water conservation areas (WCAs), WCA 1 and WCA 2A, in the Florida Everglades, USA (Fig. 1). For the hydrological record, we used EDEN version 2 daily water surface estimates for 400 x 400 m cells (Jones and Price 2007). We calculated daily water depth by subtracting ground elevation from the EDEN surface estimates. The ground elevation data came from the source data of the EDEN DEM, the High Accuracy Elevation Data (HAED) acquired by the U.S. Geological Survey (Desmond and Survey 2007; Jones and Price 2007). The HAED elevations within WCA 1 and 2A were acquired between April and December 2004. A 10-year time-series of daily water depth estimates at each HAED point was derived starting January 1st 2000 and ending May 10th 2010 in order to complete the dry season of 2009. Mean elevations of the two WCAs differ by 113 cm (WCA 1 = 417 ± 24 cm; WCA 2A = 304 ± 31 cm) (Fig. 1A).

For the co-occurring plant community information we used the brief description of vegetation at the sample location that was recorded for each HAED sample at the time of elevation data collection. We created a dataset that matched the calculated hydrology at the HAED point to a co-located vegetation type by using the descriptions to assign a vegetation community class to each point. Our plant community classification scheme was a modification of the Comprehensive Everglades Restoration Plan vegetation classification (Rutchey et al 2006; Gann et al 2012) (Table 1). Slough communities were dominated by floating and some broadleaved species (e.g., *Nymphaea odorata*, *Utricularia* spp.), as well as open water. Wet prairie communities included mainly short graminoid species, such as *Eleocharis cellulosa* and *E. elongata*, *Rhynchospora tracyi* and *R. inundata*, and *Panicum hemitomon*, as well as occasional broadleaved and floating vegetation. The *Cladium* community was dominated by *Cladium jamaicense*, while the *Typha* community was dominated by *Typha domingensis* and/or

T. latifolia. The tree and shrub classes included vegetation present in tree islands (Stone et al 2002), while the *Salix* shrub class had *Salix caroliniana* communities (Table 1). The total number of sample points was 6,051 with 3,415 in WCA 1 and 2,636 in WCA 2A.

Defining temporal extents of hydrological records: To determine whether long-term hydrologic records improved plant community class predictions, we used 2-, 4- and 10-year hydrological time-series. The 2-year period covered 2002 through 2003, i.e., the year immediately prior to the HAED vegetation data acquisition; the 4-year period began in 2000 and ended in 2003; and the 10-year period covered 2000 to 2009.

Defining start- and end-points of time intervals: To determine whether using hydrologically-defined periods, rather than annual averages, improved plant community class predictions, we examined data for periods spanning Julian years and hydrologically-defined intervals (1 hydrologic interval = 1 wet season + 1 dry season). The latter began with the wet season onset of the starting year and lasted until the end of the final dry season of the defined period. To define hydrologic intervals, we used the National Oceanic and Atmospheric Administration-defined onset and end of wet and dry seasons for south Florida (Biedinger and Lushine 1993). To consider the differences between averages across years versus variables derived from the full extent of the periods, we processed data based on Julian years, then averaged across the Julian years; for the hydrologic intervals, we processed data from the first day of the period to the last.

Defining hydrological variables and statistical descriptors: For all 6051 sampling locations, we derived water depth estimates for each location by subtracting the HAED elevation measurements from the EDEN daily stage estimates. After applying a 3-day low pass filter on the depth estimates to eliminate single-day data spikes, we determined whether the condition of the location for that day was wet or dry. We used a threshold value of +5 cm that had to be reached before a dry event switched to a wet event and -5 cm to switch from a wet to a dry event.

We used the hydrology dataset to develop hydrological variables that described the depth, duration and frequency of hydrological events. Water depth variables during wet events included the mean, median and maximum water depths. Hydroperiod length variables were the maximum number of consecutive dry or wet days and the total number of wet days for a given time interval. Hydroperiod frequency was expressed as number of distinct wet events during the time period under consideration. Each of these variables was computed for the 2-, 4- and 10-year periods and for both the Julian years and the hydrologic intervals, for a total of 42 hydrologic variables.

Analytical methods for variable selection: To select hydrological variables to use in defining plant community hydrology, we used classifier performance for subsets of variables to determine their suitability in differentiating plant communities. Since vegetation abundance along hydrological gradients is not expected to be normally distributed, we used a non-parametric classification algorithm based on the recursive partitioning and random forest principles pioneered by Breiman (Breiman 2001). It has been demonstrated that the incorporation of random forest techniques in vegetation distribution models can lead to improved predictive models when compared to models based on the generalized linear model framework (Peters et al 2007).

We considered three hydrologic variable types (depth, length and periodicity) for each of the two types of hydrological periods (Julian year averages vs. hydrological intervals) and three record lengths (2-yr. vs. 4-yr. vs. 10-yr.) to create a total of 18 models. Variable selection was performed in two steps. We first evaluated classification model accuracies for subsets of variables. In a second step we determined the best variables within the subsets of the best models. Model performance was evaluated based on out-of-bag (oob) error for each model; this is an unbiased estimator of classification error for a given model and can be compared among models (Breiman 2001). In order to build confidence in the model selection process, for each model we sub-sampled the full data set with replacement for 20 iterations, selecting a randomly stratified sample of 20% of the data for each iteration. The significance of differences between models was evaluated for pairwise model oob-error estimates using an analysis of variance (ANOVA).

We utilized the random forest algorithm implemented in the R package randomForest (Liaw and Wiener 2002). For each iteration of samples we built 500 trees (ntree = 500) using a randomly selected variable for each node (mtry = square root of the number of variables), and recorded the oob. For the best depth and length variable models, we determined the most important variable based on the unscaled (scale = FALSE) (Strobl et al 2007) mean decrease in accuracy across all 20 iterations of each model. We evaluated the significance of the mean decrease in accuracy of each variable with an ANOVA. With the three selected hydrological variables, we established a classifier for individual datasets of WCA 1 and 2A and for the pooled data to determine overall accuracy estimates for the three classifiers.

Analytical methods for determining realized plant community optima and tolerances: To interpret the distribution of plant communities along each of the three selected hydrological variable gradients, we generated probability density plots for each class (area under each community class curve = 1) (Bowman and Azzalini 2014). These plots showed the distribution of each class along the hydrological gradient. We derived estimates of community hydrologic optima and tolerances as summary statistics from these density estimates (Hintze and Nelson

1998; Adler 2005). We interpreted optimal conditions for each class as the value of maximum density, but we also present the class median. For realized tolerance estimates we used the 5th and 95th percentiles of the community class density distributions.

Using the density distributions, we derived two proportions that quantified proportional plant community distributions along the hydrologic gradients: the conditional density and the density deviation. These proportions provide information on community occurrence in relation to other communities along the gradients. The conditional density is the proportional abundance of a community in relation to all other community classes for every point on the hydrologic gradient. Conditional density translates into proportional abundance estimates along the gradient that sum to 1 for each estimate (sum of all curves at each point along the gradient = 1). When the conditional density curves for each class are plotted together, they show which communities share portions of the hydrologic gradient and provide probability estimates for the presence of each community at every point along the gradient.

The second proportion, the density deviation, is the deviation of the conditional density from the density expected if the hydrological variable had no effect on community presence. Thus, the null hypothesis is that at each point along the gradient, a community is present at its proportional abundance across the entire landscape (i.e., abundances given in Table 1). The density deviation for a class equals the conditional density at a point along the gradient minus the proportional abundance for that class across the landscape. The density deviation indicates where a plant community is over- or underrepresented along a gradient when compared to its proportional abundance across a region. If the conditional density of a class is greater than its landscape proportional abundance, then the density deviations are positive and the class is overrepresented for that portion of the gradient. If the density deviations are negative, then the class is underrepresented. Areas above zero on the density deviation plots can be interpreted as relative optima (performance better than expected), in contrast to optima estimated from the maximum density of a community along the hydrological gradient.

For each of the three selected variables, we generated vegetation-class-specific density estimates, conditional density estimates, and density deviation estimates along the hydrological gradients. Distribution of these estimates were compared for communities within each conservation area using a Kruskal-Wallis test, while distribution of community classes across WCA 1 and 2A were compared using *k*-sample Anderson-Darling tests (Scholz and Zhu 2012). For the Anderson-Darling tests, we combined the density distributions from both WCAs and then tested whether the distribution from each WCA was a subset of the combined distribution.

Processing the hydrological variables from time series records, as well as all data analysis and graphing, was performed in R (x64 v. 3.0.2) (R Development Core Team and R Core Team 2013). Maps were created in ArcGIS (ESRI 2011).

RESULTS

Comparison of community distributions by region: Plant community class frequencies differed significantly between samples from the two regions (Table 1) (contingency table analysis $\chi^2 = 856$, df = 5, $p = 0.000$). WCA 1 had more slough, wet prairie and trees/shrubs than expected, while WCA 2A had more *Cladium* and *Typha*. Only *Salix* occurred at similar frequencies in samples from the two areas. *Cladium* was the most abundant community class in both regions, although this class was 1.8 times more abundant in WCA 2A than in WCA 1. The second most abundant class differed between the two WCAs, being wet prairie in WCA 1 and *Typha* in WCA 2A (Table 1, Fig. 1B).

Hydrologic variable selection: When comparing models for annual Julian years vs. hydrologic intervals for WCA 1 and 2A combined and for all time periods, the classification models for hydrologic intervals performed better (had lower oob-errors) than those for annual Julian years. Differences in errors between model types were significant in 7 of 9 comparisons (ANOVA, $p \leq 0.05$, $N = 20$), with the Julian years having greater errors in 6 of those cases. Similar results were found when comparisons were made in WCA 1 or 2A individually. We thus used hydrologic intervals in subsequent variable selection.

When comparing the 2-, 4-, and 10-year periods using hydrologic intervals, models were not significantly different between periods for the water depth variables, but the six models using hydroperiod length and the number of events had significant differences between periods (ANOVA, $p \leq 0.05$, $N = 20$). In these cases, the longer period (either 4- or 10-year periods) had lower out-of-bag errors, with two exceptions: the 4-year period was better than the 10-year period for number of periods, while the 2-yr period out-performed the 10-year period for the same variable. When similar comparisons were made for WCA 1 or 2A alone, periods either were not significantly different (4 of 18 comparisons) or the longer periods had lower errors, with the exception of the 4-yr period out-performing the 10-yr period for the number of wet events. In these comparisons among models for each WCA, comparisons between models using the 4- and 10-yr periods were not significant in three cases, the 4-yr period was better than the 10-yr period in two cases, and the 10-year period was better than the 4-yr period in one case. Because of this lack of clear differentiation between the 4- and 10-year periods and uncertainty about how well our vegetation data, which was sampled at the end of the 4-yr period (2003), reflected vegetation at the end of the 10-yr period (2009), we chose the 4-yr period for further variable selection.

When comparing among water depth variables using the 4-yr hydrologic interval for both WCAs, the maximum water depth had the greatest mean decrease in accuracy (21.6%), followed by the median water depth (19.7%), then the mean water depth (14.6%). In comparisons of hydroperiod length variables using the 4-yr hydrologic interval for both WCAs, the maximum length of wet events had the greatest mean decrease in accuracy (20.8%), followed by the total number of wet days (16.1%), then the maximum dry period (15.9%).

Because we wanted to compare plant community hydrology using one of each of the three variable types, we chose the best-performing water depth variable (maximum water depth) and hydroperiod length variable (maximum wet period), along with the single event frequency variable (number of wet events) and used the 4-yr hydrologic interval for all of them. A random forest classification model based on these 3 variables had an overall accuracy of 53% when data was pooled across both areas with higher accuracy of 60% for WCA 2a and a slightly lower accuracy of 52% for WCA 1 when evaluated by individual regions. For the pooled data the maximum length of wet events had the largest mean decrease in accuracy (14%), followed by the maximum water depth (12%), then the number of wet events (9%). In WCA 1 the maximum length of wet events and maximum water depth variables had a comparable importance (mean decrease in accuracy of 13%), while number of wet events had a decrease of 7%. In WCA 2A the number of wet events and maximum water depth had equal mean decrease in accuracy

(10%), while the more important variable was maximum length of wet events with a mean decrease of 13%.

Hydrological conditions in WCA 1 and WCA 2A: Regions WCA 1 and WCA 2A had different but overlapping hydrological ranges, as seen in the distribution of inundation depth, inundation length and frequency of wet events (Fig. 2). All three variables were significantly different ($p \leq 0.05$; Anderson-Darling) between WCA 1 and WCA 2A.

Plant community density distributions for maximum water depth: Maximum water depths for plant communities ranged from shallowest for trees/shrubs through *Cladium*, *Salix* and wet prairies, to deepest for *Typha* and sloughs, as quantified by class maximum densities (Table 2; Fig. 3-A, 4-A). The distribution of communities along maximum water depth gradients were significantly different ($p \leq 0.05$; Kruskal-Wallis) for both WCAs for almost all class pairs. The exceptions in WCA 1 were *Cladium* compared to *Salix* and wet prairie; *Salix* compared to wet prairie; and *Typha* compared to slough. In WCA 2A distributions were not different for trees and shrubs compared to *Cladium, Salix*, *Typha* and wet prairie; *Cladium* compared to *Salix*; and *Typha* compared to wet prairie. The only community that differed from all others in WCA 2A was slough.

Conditional densities for communities in the two WCAs showed that the proportional abundance of the communities differed significantly from the pooled proportional abundance except for *Salix* and *Typha* in WCA 2A ($p \leq 0.05$; Anderson-Darling). In WCA 1, maximum water depth below ~ 50 cm were dominated by trees/shrubs, between ~ 50 – 80 cm by *Cladium* and wet prairies, and above 80 cm by sloughs (Fig. 4-1B); *Typha* and *Salix* were not dominant at any water depths. A similar pattern was observed for deviation from the conditional density (Fig. 4-1C) under the null hypothesis, except *Cladium* was underrepresented at maximum depths

> 100 cm, where sloughs started to dominate and were encountered more frequently than expected based on the distribution under the null hypothesis (Fig. 4-1C).

In contrast, conditional densities and density deviations in WCA 2A showed that trees/shrubs were dominant and overrepresented compared to the null hypothesis only at very shallow (< ~ 10 cm) maximum water depths (Fig. 4-2B, C). *Cladium* was dominant from 10 to ~ 125 cm water depths (Fig. 4-2B), even though it was overrepresented over this range only between ~ 10 and 70 cm (Fig. 4-2C). Although never dominant, wet prairies were overrepresented at greater depths than in WCA 1 (Fig. 4-2B, C).

Plant community density distributions for hydroperiod length: Class distributions for maximum length of wet events were multimodal and more variable within each class in WCA 1 than in WCA 2A (Table 2; Fig. 3-B; Fig. 5-A). Greatest densities for the maximum wet event length varied from 1,110 days for sloughs to 312 days for trees/shrubs in WCA 1 and from 1,474 days for sloughs to 246 days for *Salix* in WCA 2A (Table 2). In WCA 1 the distribution of the communities along this gradient differed for all classes ($p \leq 0.05$; Kruskal-Wallis) except *Cladium* vs. *Salix*, *Typha* vs. wet prairie, and *Salix* vs. trees/shrubs. In WCA 2A *Typha* did not differ from *Cladium*, and *Salix* did not differ from trees/shrubs ($p \geq 0.05$; Kruskal-Wallis). In WCA 1 the optimal maximum wet event length for *Typha* was comparable to sloughs, whereas in WCA 2A, it was more similar to *Cladium*.

Conditional densities between WCAs were significantly different for all communities ($p \leq 0.05$; Anderson-Darling) except for trees/shrubs in WCA 1. In WCA 1 trees/shrubs dominated and were overrepresented compared to the null hypothesis at maximum wet events less than ~ 500 days; *Cladium* dominated from ~ 450 to 900 days and was overrepresented from ~ 250 to 900 days; wet prairies dominated between ~ 900 and 1300 days; and sloughs dominated when the maximum wet event was greater than ~ 1300 days (Fig. 5-1B, C). In contrast, in WCA 2A *Cladium* dominated throughout the hydrologic gradient and was overrepresented compared to the null hypothesis at maximum wet events between ~ 450 to 1250 days (Fig. 5-2B, C). Although *Typha* was never dominant in WCA 2A, it was overrepresented compared to the null hypothesis at maximum wet events less than ~ 500 days and, along with the slough community, at > 1300 days. Wet prairies were overrepresented at > 500 days, while the tree/shrub and *Salix* communities were not overrepresented anywhere (Fig. 5-2B, C).

Plant community density distributions for number of wet periods: Differences among communities in distribution of the number of wet events in the 4-year period were significant ($p \leq 0.05$; Kruskal-Wallis) except for *Salix* vs. *Cladium* and trees/shrubs, and *Typha* vs. wet prairie in WCA 1, and for *Cladium* vs. *Typha*, and *Salix* vs. trees/shrubs in WCA 2A. Similar to maximum water depth, variation in number of wet periods was greater in WCA 2A than in WCA 1 (Table 2; Fig. 3-C).

In WCA 1 *Typha* and sloughs had maximum densities at sites with < 2 wet events during the 4-year period (i.e., extended periods without dry-downs), while wet prairies were most abundant at sites with 3 wet events (Table 2). *Cladium*, *Salix* and trees/shrubs had maximum densities at sites with 4 wet events (i.e., sites that dried down every year). In WCA 2A, while sloughs had maximum density at 1 wet event (sites that never dried down), *Typha* resembled *Cladium* and wet prairies with an intermediate number of wet events of 3 to 4, and trees/shrubs and *Salix* had maximum densities of 5 wet events (Table 2).

The length of the temporal record for the number of wet periods had a large effect on the utility of this variable in differentiating community classes. The 4-year interval differentiated sloughs, wet prairies, *Cladium* and trees/shrubs (Fig. 6-1), whereas the 2-year interval did not

(Fig. 6-2). In both WCAs the plant communities had distinct conditional density ranges in the longer temporal record (Fig. 6-1B) for all communities ($p < 0.05$; Anderson-Darling); these distinctions were not apparent in the 2-year record (Fig. 6-2B).

DISCUSSION

Plant community hydrology descriptors: The density-based approach to hydrology descriptors provided an exhaustive quantitative description of the hydrologic environment of each plant community. This approach was made possible by the large, spatially-explicit, co-located vegetation and hydrologic datasets that provided a means to statistically describe and compare plant community hydrology. Our spatially exhaustive quantitative approach to realized plant community optima and tolerances improves on prior descriptive approaches that relied on small numbers of measurements because it captures the entire range and distribution of hydrologic conditions in situ. Todd et al. (2010) used a similar approach to explore vegetation/hydrology relations in Everglades National Park, FL, USA. Their correlations, however, were indirect because they superimposed vegetation classified at a 20 x 20 m scale on hydrologic grids that were 400 x 400 m, thus losing hydrological variation between communities within the 400 x 400 m cell. The power of the approach, however, was illustrated by their ability to separate broad community classes based on hydrology despite this limitation. We were able to generate more precise estimates for plant community hydrology because vegetation and hydrology were more accurately co-located, were at the same resolution (the HAED point), and were at the scale of a single community class.

Realized plant community hydrological optima and tolerances: Our large datasets enabled us to examine plant hydrological requirements in new ways. We quantified plant community hydrological optima in two ways: maximum density and conditional density/density deviations. Given the non-normal distribution of the hydrological variables, the maximum density is a more appropriate estimate for optima than the mean and standard deviation. The maximum density shows where a community is most common along a hydrologic gradient; the conditional density provides a picture of how a particular community relates to other communities along the gradient, indicating the importance of non-hydrological factors; and density deviations indicate where communities are over- or underrepresented when compared to their proportional abundance estimates across the landscape. Although we have used these density-based approaches to quantify vegetation responses to hydrology, they could be applied to vegetation responses along any environmental gradient where there is sufficient data to support robust density estimates.

Our density-based descriptors showed the wide range of realized tolerances to hydrologic conditions by these different communities, as well as the large degree of overlap among communities. The data also suggest that realized plant community hydrologic optima and tolerances in a natural environment depend on the environmental context and likely will differ from species-specific optima and tolerances derived from laboratory or mesocosm experiments. The realized niche space for a plant community within a geographic region is limited by the distribution of actual hydrological conditions and by other environmental factors, such as nutrients, as well as by biotic interactions. The realized conditions are space-time dependent and result from the interactions of these biotic and abiotic factors. The conditional density and density deviation estimates developed here provide ways to describe these combined effects on plant community distribution and will facilitate the development of better vegetation distribution models that include factors such as nutrients, disturbance history and biotic interactions.

Our quantitative approach provides insights that could be missed by qualitative descriptions of community distributions of proportional abundance along a hydrologic gradient. For example, in this study WCA 2A had a much greater abundance of *Cladium* and *Typha* communities than WCA 1, balanced by decreased abundance of almost all other community classes. The two WCAs have different water management regimes (Fennema et al 1994; Light and Dineen 1994) and different nutrient inputs. In particular, WCA 2A receives excess phosphorus (DeBusk et al 2001), which is the limiting nutrient in the historic Everglades (Craft et al 1995; Noe et al 2001; Childers et al 2003; Gaiser et al 2005). These additional abiotic differences have led to differences in plant community abundances and distributions, reflected in different patterns of conditional density and density deviations for *Cladium* and *Typha* along hydrologic gradients in the two WCAs. The conditional density and density deviation thus reflect the different realized hydrological optima and tolerances that these communities have in the two WCAs.

Our results show that community distributions along hydrological gradients do not generalize across entire landscapes. Differentiation of communities based on hydrological variables is therefore not necessarily highly predictable from one region to the next, i.e., the response of vegetation to particular hydrologic regimes cannot be applied globally to predict plant communities in other regions of the same wetland landscape. Similarly, Ross et al. (2003) found large differences in plant community hydrology among regions in Everglades National Park, and Givinish et al. (2008) found differences in hydrology of the same communities among northern and southern WCA 3A and WCA 3B. These results provide a cautionary tale for restoration performance measures based solely on hydrology, as they suggest that the hydrologic target for a specific outcome may change across a landscape, depending on other biotic and abiotic factors.

Effectiveness of hydrological variables in predicting plant communities: The hydrological variables developed here were better predictors of plant community class than traditional measures of hydrology such as annual average water depth. Although mean water depth is often used to describe plant species or community hydrology (Wood and Tanner 1990; Ross et al 2003; Childers et al 2006), the mean water depth variable in our study performed relatively poorly in predicting vegetation class, even when calculated as the mean of wet events only. Thus, although mean water depth provides a description of one aspect of community hydrology, it is not the most suitable hydrologic indicator for plant community distribution. A better measure of water depth was the maximum depth, which reflects depth tolerances and thus community tolerances to hydrologic stress. For aquatic vegetation, these tolerances are hypothesized to depend on species' physiological limitations at the deeper ends but biotic interactions at the shallower ends of the species' hydrologic ranges (Keddy 2000; Givnish 2002).

Another good hydrological variable in our analysis was the maximum length of the wet event, a hydroperiod length variable. Although hydroperiods have been defined in various ways (Ross et al 2003; Childers et al 2006; Givnish et al 2008; Zweig and Kitchens 2008; Todd et al 2010; LoGalbo et al 2013), they are usually calculated as annual means. In our study, use of environmentally-defined hydroperiods (the hydrologic interval) enlarged the hydrological description by allowing the length of the wet or dry event to extend over several years when appropriate.

Although the number of wet events had the lowest mean decrease in accuracy when predicting plant communities, this type of variable improved with the length of the hydrologic record and varied in importance by region. The 10-year record for this variable more clearly separated communities in the conditional density plots than the 2- or 4-year records, suggesting that this variable could become more useful with even longer time-series.

Some degree of overlap and classification inaccuracy in predicting vegetation from hydrology can be attributed to limited data accuracy and uncertainty. Analytical results of hydrological time-series processing are affected by the accuracy of the water surface estimates, which was ±5 cm for the EDEN dataset (Palaseanu and Pearlstine 2008; Liu et al 2009), as well as by the accuracy of the elevation measurements, which had an accuracy estimate of ±15 cm (Desmond and Survey 2007). These errors propagated to our derived estimations of wet and dry event lengths and frequencies. For the 10-year record, we further assumed that the data points did not change their community class membership. Nevertheless, the large number of data points and the use of density estimates provide a relatively high confidence in the overall pattern of the results, and such errors should affect the entire dataset equally, so differences between particular communities or regions should represent other factors.

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TABLES

Table 1. Community class descriptions and the distribution of samples by community classes in percent. The number of samples in WCA 1 and WCA 2A were 3,415 and 2,636, respectively.

Community Descriptor	WCA 1&2a	WCA 1	WCA 2A	Community	WCA 1&2a	WCA 1	WCA 2A
open water slough	1.69	1.29	2.2	Slough	13.09	18.27	6.37
floating slough	10.78	16.98	2.73				
broadleaf slough	0.63	0	1.44				
floating wet prairie	5.77	0	13.24	Wet Prairie	21.25	26.56	14.38
short graminoid wet prairie	15.49	26.56	1.14				
Cladium tall graminoid	40.27	29.4	54.36	*Cladium*	40.27	29.4	54.36
Typha tall graminoid	13.27	8.67	19.23	*Typha*	13.27	8.67	19.23
Salix shrub	2.68	2.37	3.07	*Salix*	2.68	2.37	3.07
shrub	7.4	11.24	2.43	Tree/Shrub	9.44	14.73	2.58
tree/shrub island	2.03	3.48	0.15				

Table 2. Summary of hydrological variables for each plant community class by region (WCA 1 and 2A), providing 5th, 50th (Median), and 95th percentiles and the maximum density of the class-specific variable distribution (greatest width of the violin plot, Fig. 3). Variables represented are 4-year maximum water depth, maximum length of wet events, and number of wet periods. Values for WCA 1 and WCA 2A are separated by "; ".

Variable	Community	Values by Region WCA1; WCA 2A			
		5th Percentile	Median	95th Percentile	Maximum Density
4 yr. Maximum Water Depth (cm)	*Cladium*	42; 47	64; 74	95; 107	65; 74
	Typha	53; 58	86; 79	131; 125	84; 79
	Slough	60; 77	87; 106	159; 166	86; 99
	Salix	35; 50	65; 71	88; 107	65; 69
	Trees/Shrubs	18; 45	48; 73	71; 105	48; 73
	Wet Prairie	43; 51	64; 78	83; 122	64; 64
4 yr. Maximum Length Wet Events (days)	*Cladium*	300; 209	712; 678	1099; 1474	739; 619
	Typha	345; 208	1096; 697	1474; 1474	1098; 342
	Slough	706; 1099	1099; 1474	1474; 1474	1110; 1474
	Salix	232; 132	708; 285	1098; 710	708; 246
	Trees/Shrubs	105; 83	346; 292	743; 710	312; 273
	Wet Prairie	338; 303	1069; 1093	1362; 1474	984; 677
4 yr. Wet Events (count)	*Cladium*	2; 1	4; 4	5; 11	4; 3
	Typha	1; 1	3; 4	5; 10	2; 4
	Slough	1; 1	2; 1	5; 3	2; 1
	Salix	2; 3	4; 5	6; 12	4; 5
	Trees/Shrubs	2; 3	4; 5	5; 14	4; 5
	Wet Prairie	1; 1	3; 3	5; 6	3; 3

FIGURES

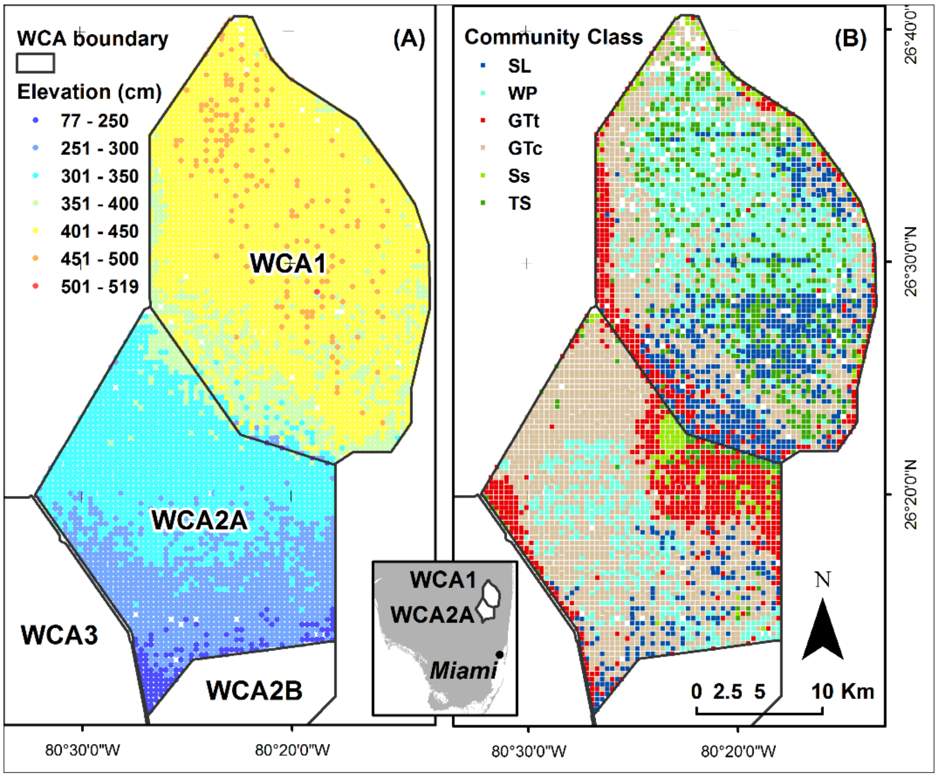

Figure 1. Elevation samples (HAED) in cm above sea level (NADV 88) (A), and spatial distribution of plant community classes associated with each elevation sample (B) for the two study areas WCA 1 and WCA 2A. There was one HAED point for each 400 x 400 m EDEN grid cell, for a total of 3415 samples within the 560 km2 of WCA 1 and 2636 samples representing the 422 km2 of WCA 2A; the combined 6051 samples covered a total surface area of 982 km2. SL = slough; WP = wet prairie; GTt = Typha; GTc = Cladium; Ss = Salix; TS = trees/shrubs.

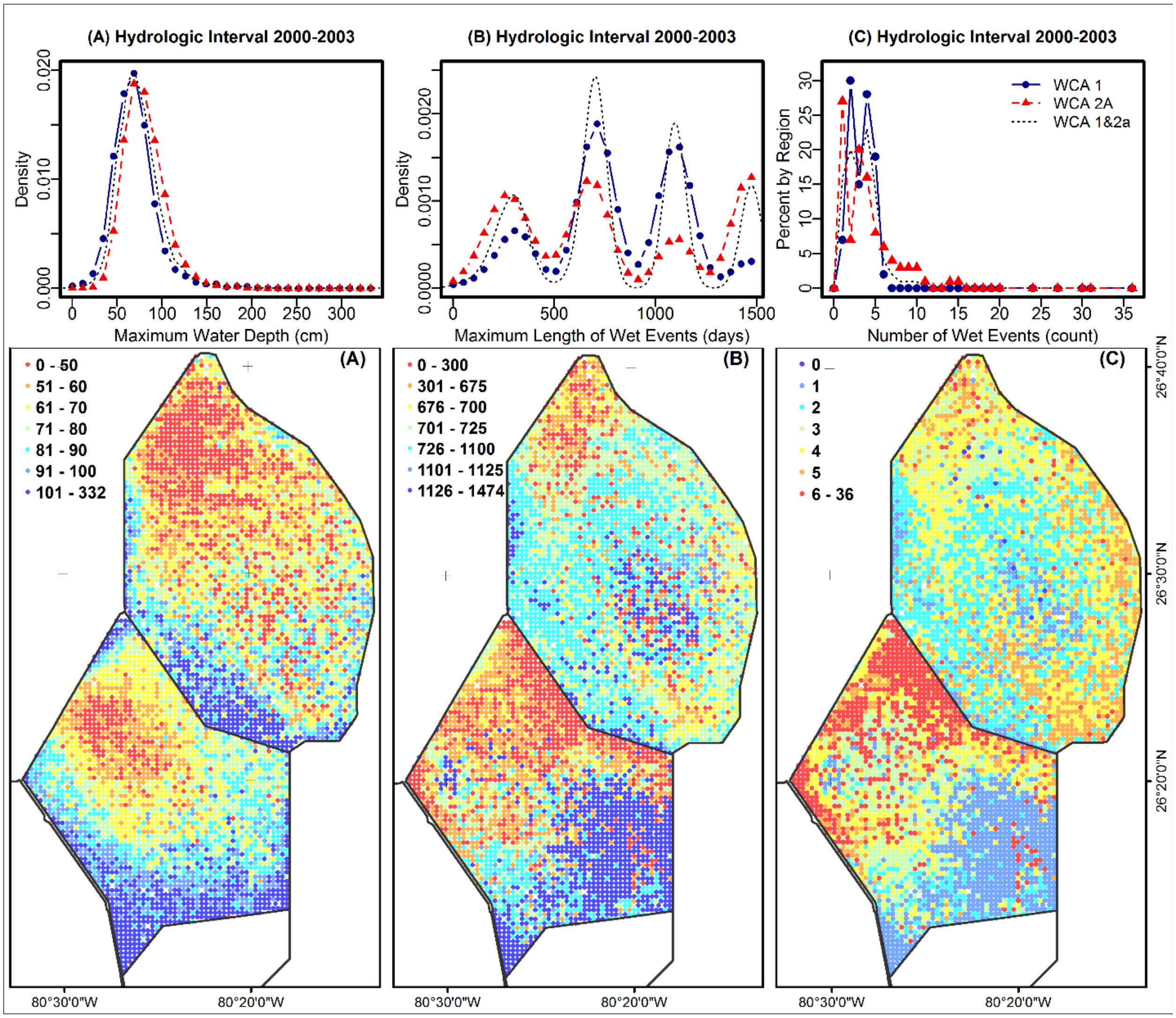

Figure 2. Distribution of hydrological environments for WCA 1 and WCA 2A given as density plots (upper panel) and maps (lower panel) for the 4-year maximum water depth (A), maximum length of wet events (B), and number of wet events (C). The maps of each variable display the data in seven quantile ranges.

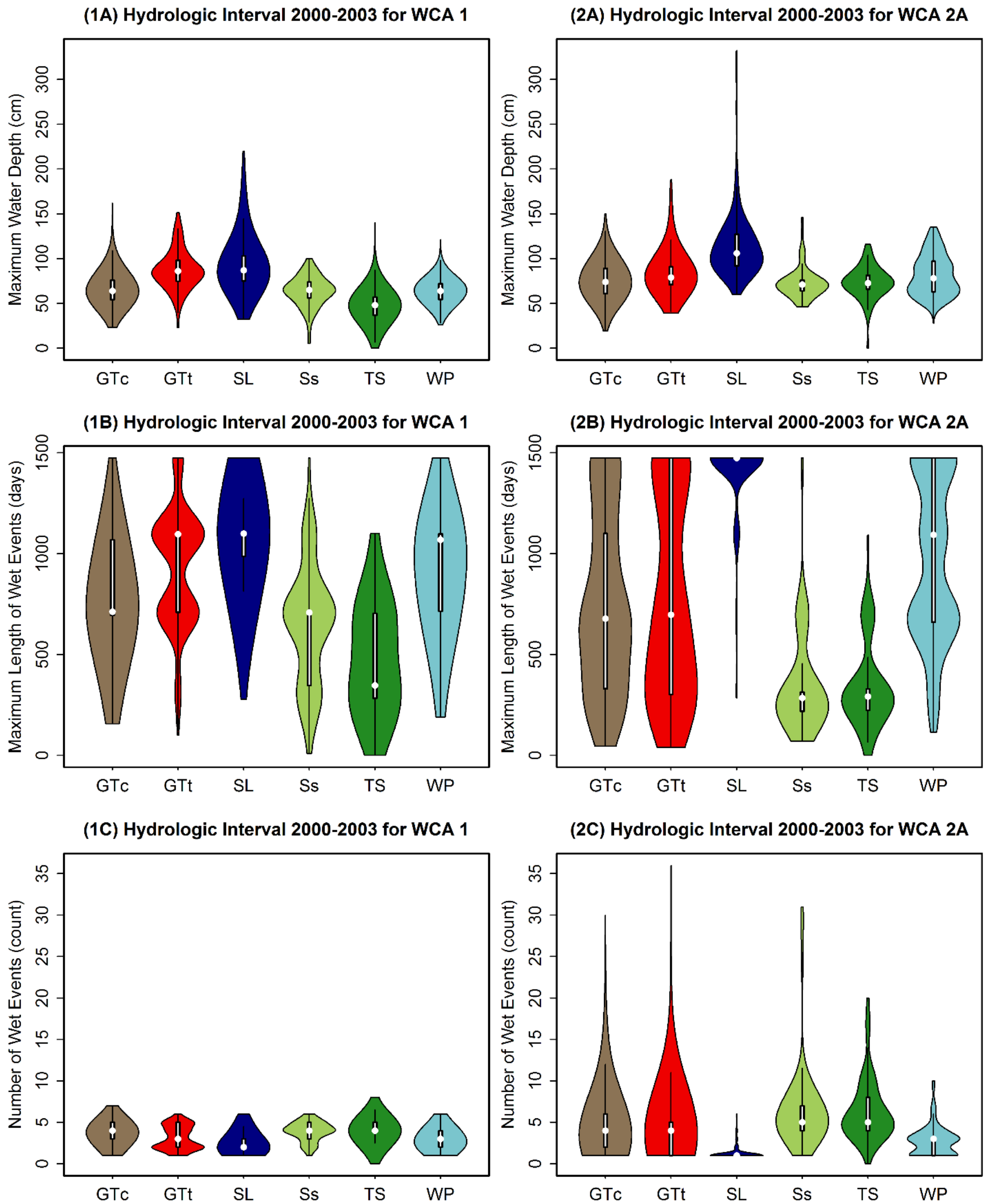

Figure 3. Distribution of plant community classes for hydrological variables given as violin plots (boxplots + density distribution) for classes in WCA 1 and WCA 2A. Estimates are for the 4-year hydrological intervals for maximum water depth in cm (A), maximum length of wet events in days (B), and the number of wet events (C). Median is indicated by the small white circle inside the violin; the 25th and 75th percentiles by the upper and lower bounds of the narrow white box; and the minimum of either 1.5 times the interquartile range or the maximum and minimum values of the data by the black lines. Community class abbreviations as in Figure 1.

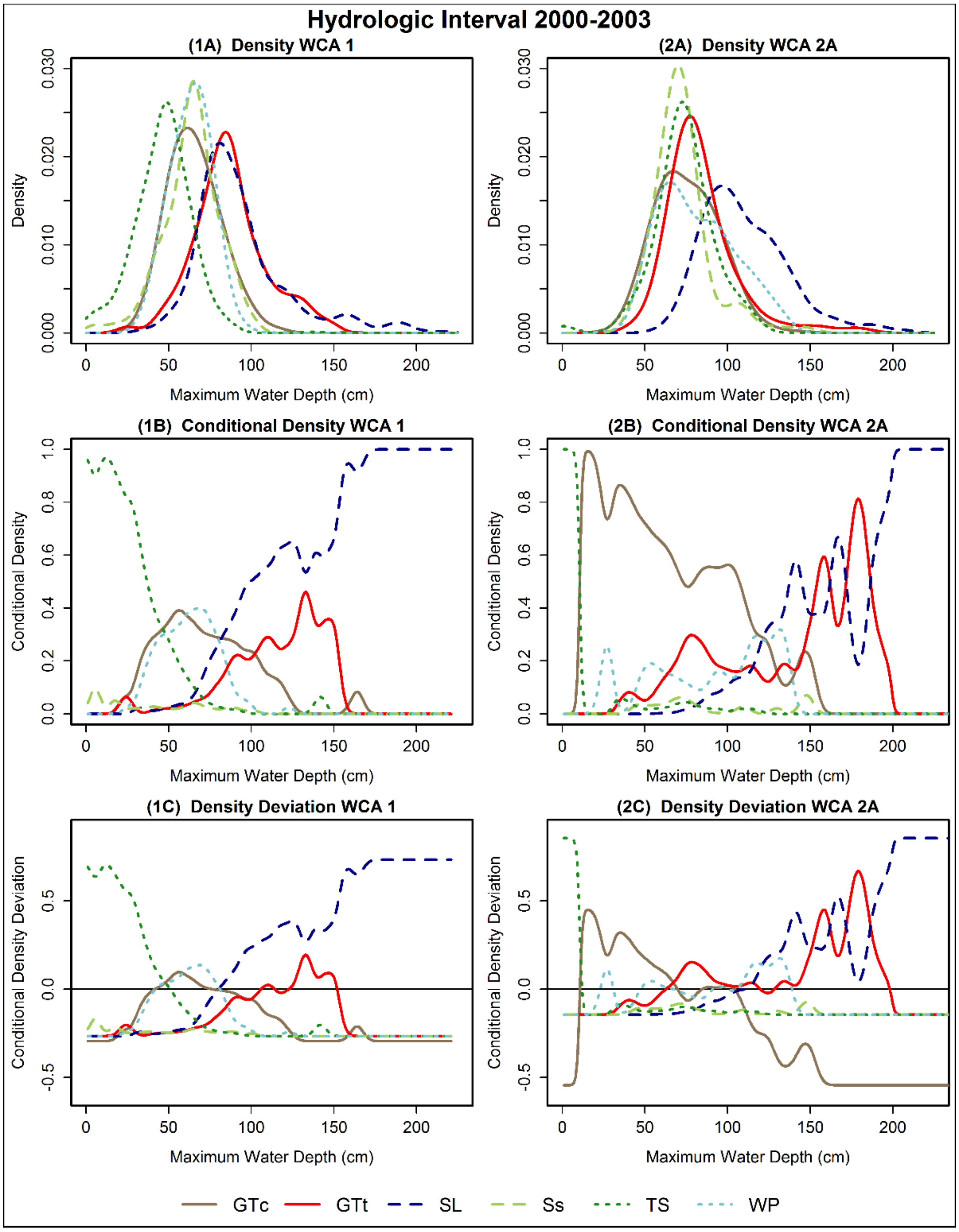

Figure 4. Density plots of the 4-year maximum water depth for the 4-yr hydrologic interval by region. A) density for each community along the hydrological gradient (sum of area under each class curve = 1); B) conditional density (at each location along the gradient, the sum of all class densities = 1); C) conditional density deviation (conditional density – proportional community abundance). Community class abbreviations as in Figure 1.

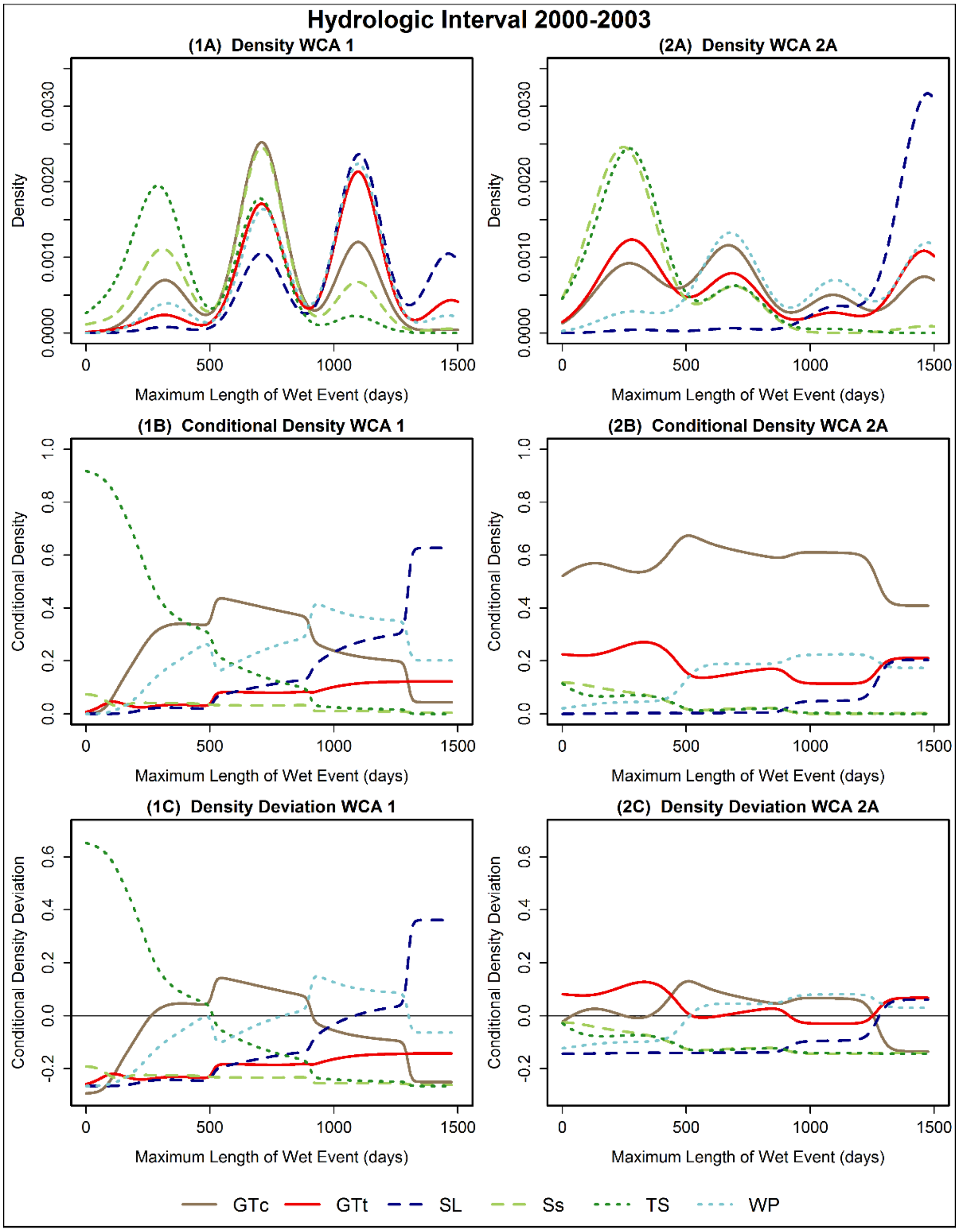

Figure 5. Density plots of the 4-year maximum length of wet events for the hydrologic interval by region. A) density for each community along the hydrological gradient; B) conditional density; C) conditional density deviation. Community class abbreviations as in Figure 1.

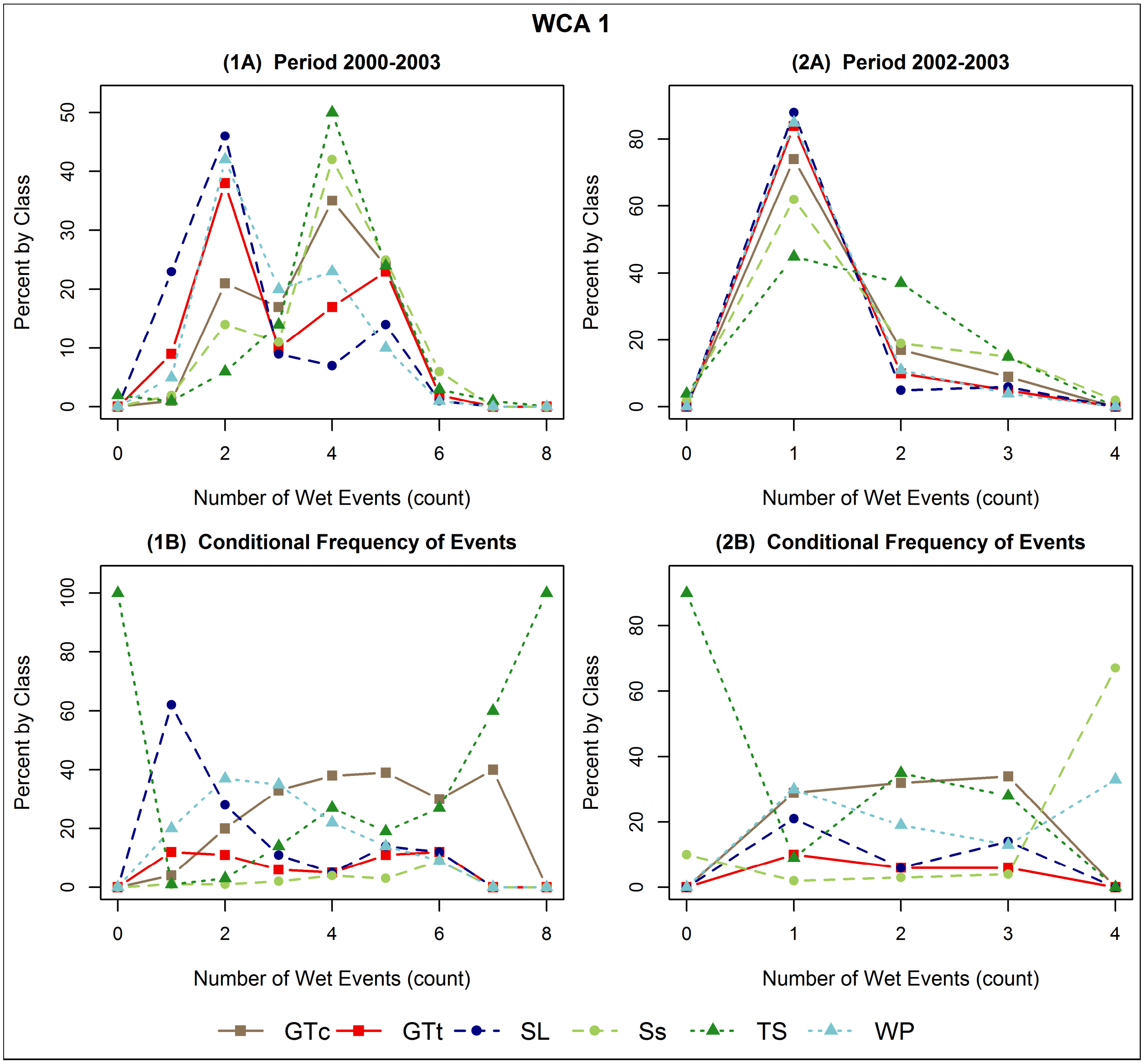

Figure 6. Comparison of number of wet events for 4-year record vs. 2-year record. A) Density for each community along the hydrological gradient; B) conditional density. The 4-year record (1A, B) shows a much better separation among classes than the 2-year record (2A, B). Community class abbreviations as in Figure 1.