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Hydrological drivers of wetland vegetation community distribution within Everglades National Park, Florida

M. Jason Todd [a,*], R. Muneepeerakul [a], D. Pumo [a,b], S. Azaele [a], F. Miralles-Wilhelm [c], A. Rinaldo [d,e], I. Rodriguez-Iturbe [a]

[a] Department of Civil and Environmental Engineering, Princeton University, Princeton, NJ 08544, United States
[b] Dipartimento di Ingegneria Idraulica ed Applicazioni Ambientali, Università di Palermo, Viale delle Scienze, 90128, Palermo, Italy
[c] Department of Civil and Environmental Engineering, Florida International University, Miami, FL 33174, United States
[d] Dipartimento di Ingegneria Idraulica,Marittima, Ambientale e Geotecnica (IMAGE) and Centro Internazionale di Idrologia 'Dino Tonini', Università di Padova, via Loredan 20, I-35131, Padua, Italy
[e] Laboratory of Ecohydrology, Faculté ENAC, École Polytechnique Fédérale, CH-1015, Lausanne, Switzerland

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ABSTRACT

The influence of hydrological dynamics on vegetation distribution and the structuring of wetland environments is of growing interest as wetlands are modified by human action and the increasing threat from climate change. Hydrological properties have long been considered a driving force in structuring wetland communities. We link hydrological dynamics with vegetation distribution across Everglades National Park (ENP) using two publicly available datasets to study the probability structure of the frequency, duration, and depth of inundation events along with their relationship to vegetation distribution. This study is among the first to show hydrologic structuring of vegetation communities at wide spatial and temporal scales, as results indicate that the percentage of time a location is inundated and its mean depth are the principal structuring variables to which individual communities respond. For example, sawgrass, the most abundant vegetation type within the ENP, is found across a wide range of time inundated percentages and mean depths. Meanwhile, other communities like pine savanna or red mangrove scrub are more restricted in their distribution and found disproportionately at particular depths and inundations. These results, along with the probabilistic structure of hydropatterns, potentially allow for the evaluation of climate change impacts on wetland vegetation community structure and distribution.

1. Introduction

The greater Everglades ecosystem is a dynamic and diverse landscape in not only its spatial extent, but also its hydrological characteristics and vegetative communities. Hydrological properties have been considered driving influences of a wetland system [18,25] and the interplay of these properties with the vegetation communities within the Everglades has been of interest for decades. Numerous studies have shown a relationship between Everglades hydropatterns and the vegetative communities found therein [2,8,17,29,37,38]. For example, sawgrass (*Cladium jamaicense*), the most widespread of Everglades vegetation communities, has been shown to favor locations with shorter duration inundation periods and more shallow depths [4,17,29]. In contrast, spikerush (*Eleocharis cellulosa*) has been shown to favor more hydric environments with greater depths [4,29]. This suggests some vegetative communities are segregated along hydrologic gradients [27,29]. Duration and depth of flooding have been cited as the major hydrologic factors controlling plant distribution [17] since due to the low slope of the Everglades region, slight changes in elevation can play large roles in the hydrology of a site [6,27]. However, others state that the role of hydrology in structuring Everglades vegetation communities remains unclear due to their interactions with a suite of other variables including nutrients, soil characteristics, fire regime and biota [4,29,37].

The temporal and spatial scales at which hydrology and vegetative structuring take place have been a topic of much study. Gunderson [17] described the hydrology of the Everglades as being affected at three different temporal scales with the slow time scale being change in sea level, the intermediate scale being the return period of droughts and floods and the fast scale being the annual hydrologic regime which is dominated by seasonal variation in rainfall. The interplay of these scales serves to complicate the relationship between vegetation and Everglades hydropatterns as larger spatial scales tend to change at a slower rate than finer ones [8]. For instance, some have shown that vegetation change in response to hydrologic alteration can be relatively rapid (i.e. a few

* Corresponding author. Tel.: +1 609 258 1436; fax: +1 609 258 2760.
E-mail address: mjtodd@princeton.edu (M.J. Todd).

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years) [2,37], while others argue that there can be a considerable time lag [14,29]. Indeed, most studies of hydrology and vegetation structuring take place at relatively narrow spatial and temporal scales making extrapolation to wider scales problematic [4]. Furthermore, the Everglades itself is a highly dynamic hydrologic system subject to natural variation and human alteration through flow control and drainage. The effects of the variable Everglades hydrology at large spatial scales and its ultimate effect on vegetation patterning remain poorly understood [37].

Recognizing the highly dynamic and diverse ecosystem that is the Everglades, we link the hydrological dynamics and their associated influences to the distribution of vegetation across the entire Everglades National Park. Our research questions include:

1) Given that hydrological processes are a forcing variable in shaping wetland communities, can we observe spatial differences in hydropatterns across Everglades National Park?
2) Are the spatial distributions of individual vegetation types structured based on the surrounding hydrologic characteristics? For instance, can we notice trends in vegetation distribution (i.e. presence/absence, frequency) based on the average hydrologic characteristics of a site?
3) Can we observe differences in hydrologic and vegetation structure by investigating these patterns at a large spatial scale of many kilometers?

These questions are of critical importance in the greater Everglades landscape as it is subject to continued human alteration and management along with the increasing threat due to climate change.

2. Methods

2.1. Study area and climate

The Everglades historically encompassed an area of over 10,000 km^2 in South Florida but today is roughly half that size with a portion of the remaining Everglades found within Everglades National Park (ENP) (Fig. 1) [8,15]. Established in 1947 and encompassing nearly 5700 km^2, it is a mosaic of different vegetative communities [8,16,19,31]. Located between temperate and tropical regions, ENP has a mixture of taxa from both regions along with locally endemic and exotic taxa. In total, the park has at least 830 vegetation taxa and includes all the major habitats found within the Everglades ecosystem [3,16].

Prior to the 1900s, the Everglades was a broad, slowly flowing wetland originating at Lake Okeechobee and flowing southward towards the Gulf of Mexico. Flow velocities are often less than 1 cm s^{-1} due to the low slope (3 cm km^{-1}) and vegetative interference. Today, the Everglades is a hydrologically altered landscape due to human action and drainage, with flow controlled through an extensive system of levees, pumps, and canals [23]. Even the area for this study, designated as a national park, is affected by these flow patterns and has been subjected to altered hydroperiods as compared to natural conditions [12,31].

Precipitation and evapotranspiration are the major natural drivers of hydrology within ENP. The climate of the ENP is described as a tropical savanna with distinct wet and dry seasons [11,20]. Over a 30 year period of record, average annual precipitation ranged from 119 to 157 cm spatially across ENP with a yearly minimum of 86 cm and a maximum of 224 cm [11]. Sixty percent of the precipitation falls between June and September with 25% falling between November and April. The months of May and October tend to be transitional with rainfall totals varying from year to year [11]. Rainfall during the wet season tends to be the result of localized thunderstorms leading to a varied distribution in time and space whereas the rest of the year is the result of large frontal systems creating a broader distribution in precipitation [11]. Evaporation from open water surfaces in the Everglades is highest in late spring with high temperatures and wind speeds contrasted against low relative humidity. In contrast, evaporation is lowest during the winter months when temperatures and wind speeds are lower. Evapotranspiration from natural ecosystems in the Everglades however is highest during the summer wet season, when temperatures are high and there is abundant water for both surface evaporation and vegetative transpiration. The lowered water table during late spring limits the actual evapotranspirative losses [11]. These rainfall and evapotranspiration patterns lead to differing

Fig. 1. Map of Everglades National Park.

overland flow patterns throughout the year, resulting in high water levels during the summertime months, a subsequent slow decline during the fall and winter months, and are followed by a rapid decline during the spring.

2.2. Hydrologic information

The water level information for this study is drawn from the Everglades Depth Estimation Network (EDEN), an integrated network that combines real time water level monitoring, ground elevation modeling, and water surface modeling to generate water depth levels of the entire freshwater portion of the Everglades [5,32]. The baseline data layer to the EDEN network is a ground surface digital elevation model developed by measurement at over 50,000 locations [9]. The water surface level data are generated into 400×400 m grid cells through the use of over 250 monitoring locations and interpolation among stations using radial basis functions with multiquadric regression [28]. Water depth is calculated as the difference between the water surface elevation model and the ground surface elevation model [5,32]. Data are organized into an ongoing daily measure of water level for the years 2000–present, but due to the timing of data release we restricted our analysis from 1/1/2000–9/30/2007. Additionally, while the entire EDEN data surface covers an area of 8192 km^2, this analysis was restricted to the area found within ENP (Fig. 1). EDEN is the longest daily measure of water level for the entire freshwater portion of the Everglades known to the authors. The EDEN model has been reported to provide an accurate high-resolution measure of water levels throughout the Everglades area [13,24]. Furthermore, Fujisaki et al. [13] showed that error was not associated with the density of monitoring gages or proximity to canals.

Using the EDEN dataset, we calculated four hydrologic measures at each 400×400 m pixel:

1) Number of hydroperiods per year;
2) Conditional mean depth (cm);
3) Mean duration of a hydroperiod (days); and
4) Percentage of time inundated.

For the purposes of this analysis, we are defining a hydroperiod as an individual inundation episode (i.e., a single wetting–drying cycle). For a given pixel, those sections of the water level time series that did not constitute a complete hydroperiod (i.e., where depth does not re-cross depth = 0 cm) were omitted. Conditional mean depth is defined as the mean depth of all inundated days (depth > 0). Mean duration of a hydroperiod is the average length of time in days for a hydroperiod, while percentage of time inundated is the number of days where there is standing water (depth > 0) divided by the total number of days.

2.3. Vegetation database

The Everglades is an area of diverse vegetation communities. For that reason, an accurate map of the vegetation communities was developed by the Center for Remote Sensing and Mapping Science at the University of Georgia and the South Florida Natural Resources Center [34]. To deal with the diversity of vegetation communities found within the study area, Welch et al. [34] developed a three-tiered, hierarchical vegetation classification system containing 79 plant community and land cover classes organized into 8 major vegetation types: forest, scrub, savanna, prairies and marshes, shrublands, exotics, additional class headings, and special modifiers [10,34]. Distribution maps of the vegetation communities were developed at 1:15,000 scale using both aerial photographs and satellite images. A polygon on the map is labeled according to the dominant vegetation type (>50%) with secondary and tertiary vegetation communities added in those areas with mixed vegetation. It is important to note that this methodology does not identify all vegetation communities present at a given location, but rather the dominant one. To verify accurate vegetation identification, ground truthing was conducted at 88 sample points across Everglades National Park using field studies, resulting in on average 90% correctness [34]. In this study, a 20×20 m grid was created and laid over the ENP study area and the dominant vegetation type extracted, producing a total of over 5 million pixels. Due to the scale difference between the two datasets, a hydrologic pixel containing the four calculated measures above can have a maximum of 400 vegetation pixels within it (Fig. 2). For example, Fig. 2 shows a single 400×400 m hydrologic pixel with a total of 400 vegetation pixels. Across the 400 pixels there are three different possible vegetation types, but each 20×20 m pixel will share the same hydrologic measures since they are part of the same 400×400 m pixel.

2.4. Analysis of hydrologic and vegetation data

The relationship between a vegetation community and the four calculated hydrological measures was evaluated by extracting out all pixels with the same dominant vegetation type and then creating histograms of the hydrologic measures. These histograms are constructed in a specific, non-traditional manner and therefore warrant some further description, which we do via an example.

Suppose that we are to create such a histogram for, say, muhly grass. Out of a total of 5,290,307 pixels in the entire study area, there are 215,170 pixels with muhly grass as a dominant vegetation type (i.e. it makes up 4.1% of the total area). Those 215,170 pixels have the values for the four calculated hydrologic measures and four histograms were then created for each of them. Let us now focus on a single hydrologic measure, conditional mean depth, as an example. We divided the mean depth values into 2-cm intervals, each of which we will refer to as a bin. Note that the number of bins for a given hydrologic measure was kept consistent across all vegetation types to ensure fair interspecific comparison. The muhly grass pixels with mean depth falling into 0–2 cm would be considered belonging to one bin or class, 2–4 cm to another bin and so forth. The height of the bar

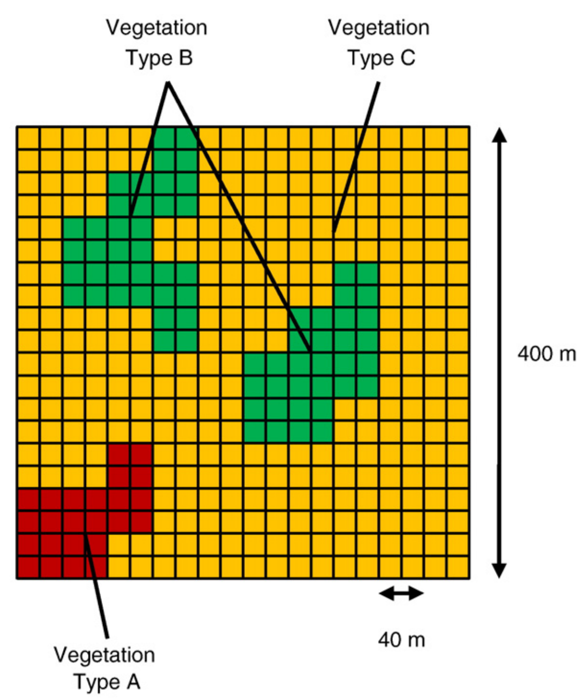

Fig. 2. Example of a single hydrologic pixel overlaid by the 20×20 m vegetation database. The single 400×400 m hydrologic pixel has 400 20×20 m vegetation pixels. An individual vegetation pixel could have one of three possible vegetation types, but all 400 pixels in this square will share the same calculated hydrologic measures.

in each bin of the histogram is the relative abundance, which is simply the ratio between the number of muhly grass pixels in that bin and the number of all pixels in the same bin. For instance, in the 8–10 cm mean depth bin, there are 269,779 pixels in the entire landscape (out of 5,290,307) and 41,540 muhly grass pixels that belong to this bin (out of 215,170), resulting in the relative abundance of 0.154 (=41,540/269,779; see arrow in Fig. 6b). It is important to note that if the muhly grass pixels were randomly distributed (i.e., without any hydrological preference), the relative abundances in all bins would be equal to 0.041. Therefore, the difference between the relative abundance in each bin and the landscape-averaged value 0.041 may be used as a signature of hydrological preference.

In an effort to quantify this concept of hydrological preference, we developed a metric we call a selectivity index (SI) to accompany these histograms. For a vegetation type, four SI's, one for each hydrological measure, were computed. The SI is given by the equation:

$$SI = \frac{1}{c}\sqrt{\frac{\sum_{i=1}^{n}(b_i-c)^2}{n}} \tag{1}$$

where n is the number of populated bins in the histogram of a given hydrologic measure; b_i is the relative abundance of the ith bin (bars in Figs. 6–8); and c is the relative abundance of a given vegetation type across the entire ENP (red line in Figs. 6–8). Despite their very similar appearances, SI is not the more traditional coefficient of variation and must be interpreted according to the concept described in the previous paragraph. Specifically, low values of SI suggest that the vegetation community has little preference or is insensitive to that particular hydrological measure, while high values suggest otherwise. In an extreme case in which pixels of a given vegetation type are truly randomly distributed with no hydrological preference, all relative abundances equal the landscape average, namely $b_i = c$, leading to SI = 0. Note that although the absolute values of SI are contingent on the numbers of histogram bins, they still allow for fair and useful comparison when the numbers of bins were kept consistent across all vegetation communities as done in this study.

3. Results

A total of over 13,000 400 × 400 m pixels make up the hydrologic dataset found within ENP (Fig. 3). Values for all four hydrologic measures varied spatially across the landscape with number of hydroperiods per year averaging 2.86, ranging between 0 and 52.1 hydroperiods per year, and values between 2 and 3 hydroperiods per year being the most frequent (Fig. 4a). The conditional mean depth averaged 22.7 cm across the landscape, ranged between 0 and 102.1 cm, and followed a bimodal distribution with values between 6–8 cm and 24–26 cm being the most frequent (Fig. 4b). Mean hydroperiod duration averaged 143.6 days, ranged from 0 to 2830 days, and was most frequent between 0 and 50 days (Fig. 4c). Across the landscape, a total of three pixels were never flooded and

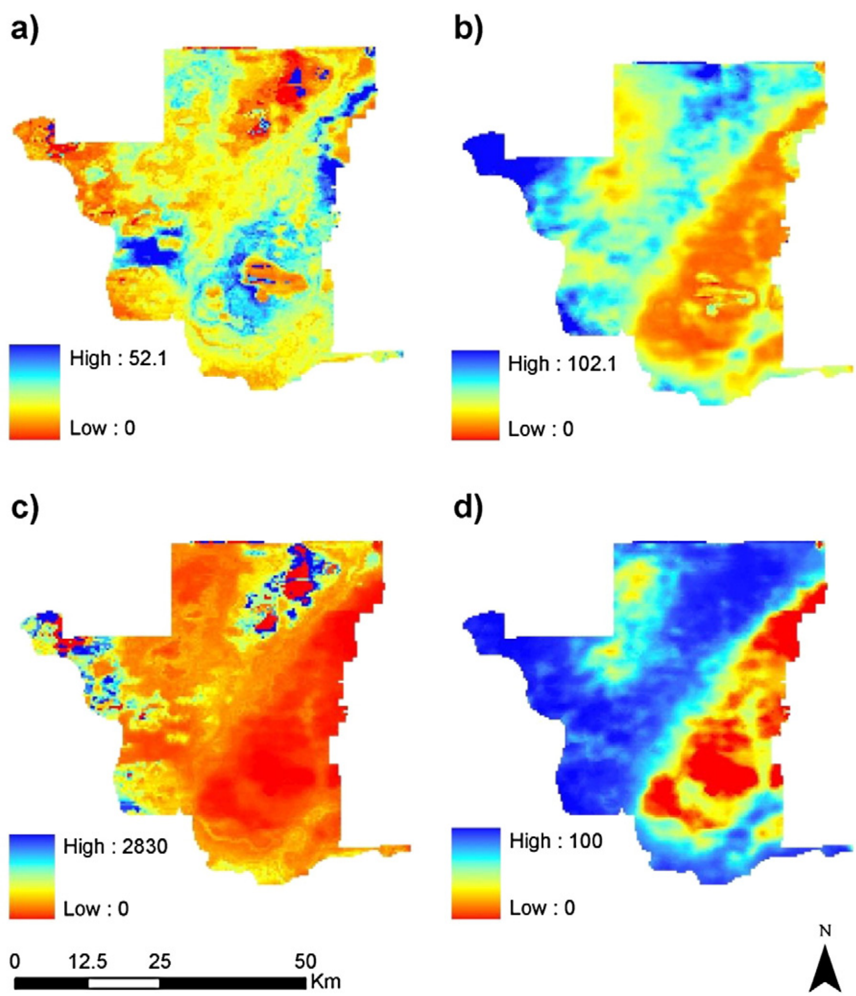

Fig. 3. Spatial distribution of (a) number of hydroperiods per year; (b) mean depth; (c) mean duration per hydroperiod; and (d) percent time inundated across Everglades National Park.

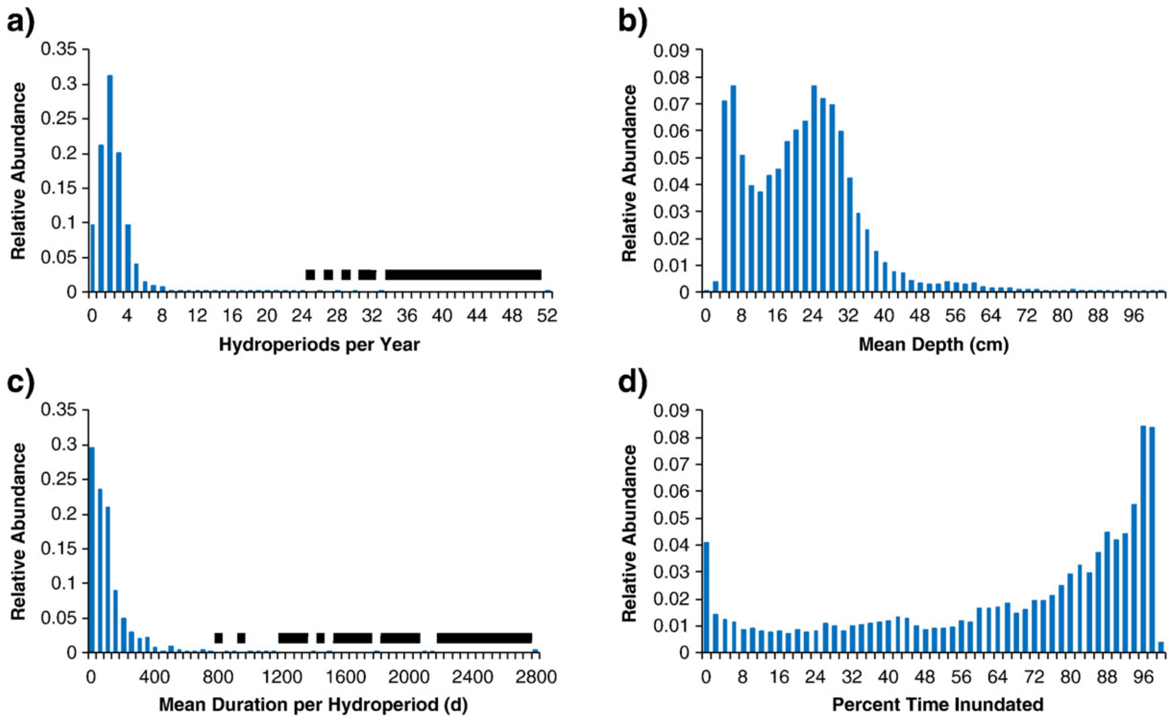

Fig. 4. Relative abundance of (a) number of hydroperiods per year; (b) mean depth; (c) mean duration per hydroperiod; and (d) percent time inundated across Everglades National Park. Black bars indicate bins which there were no data.

assumed to have a conditional mean depth of zero for the vegetation analyses. The large upper bound for the mean hydroperiod duration is due to some pixels remaining inundated for the entire study period. Percent of time inundated averaged 66.9%, ranged from 0 to 100%, with 96–98% the most frequent class (Fig. 4d). While not the most frequent class, a large number of pixels is observed at percent time inundated between 0 and 2% indicating there are a large number of locations that are rarely to never flooded.

The mean depth and percent time inundated appear to be more appropriate for the following analysis to relate vegetation and hydrology as they are more regularly distributed and have data within every bin (Fig. 4). The other two hydrologic measures, namely the number of hydroperiods per year and the mean duration, have bins in which no data are found (black bars in Fig. 4a and c). Therefore, for the purposes of this paper we focus our discussion and analysis on the mean depth and percent time inundated. The joint probability surface for these two measures shows that at either extreme of percent time inundated (i.e., rarely inundated or inundated most of the time), there are a wide range of mean depths (Fig. 5), suggesting a weak dependence between the two measures at these ranges. In contrast, over the intermediate values of percent time inundated, the range of mean depths is relatively narrow and thus a stronger correlation is found.

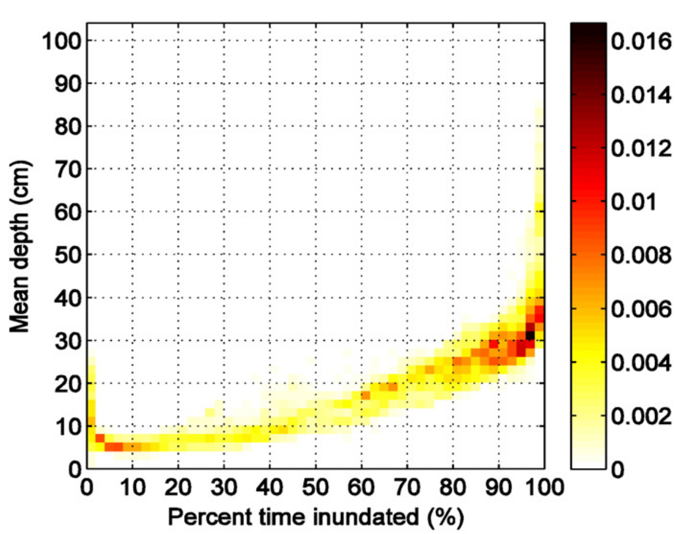

Fig. 5. The joint probability surface of percent time inundated and mean depth. The value of each pixel represents the relative frequency of all pixels across Everglades National Park meeting both hydrological conditions.

ENP is a diverse landscape assemblage of different vegetation communities with a total of 52 different vegetation types (out of a possible 79 for the entire Everglades). A total of 56 community types were identified, but four were listed as community types having no vegetation ("Canals", "Roads", "Structures and Cultivated Lawns", and

Table 1
Percent coverage of dominant vegetation types found within Everglades National Park.

Vegetation type	% Coverage
Sawgrass	60.7
Mixed graminoids	6.5
Tall sawgrass	5.8
Muhly grass	4.1
Spike rush	3.0
Red mangrove scrub	2.2
Bayhead	1.7
Pine savanna	1.6
Willow shrublands	1.5
Dwarf cypress	1.5
Bay-hardwood scrub	1.4
Brazilian pepper	1.2
Cattail marsh	1.1

Only those vegetation types constituting more than 1% of the total landscape are listed.

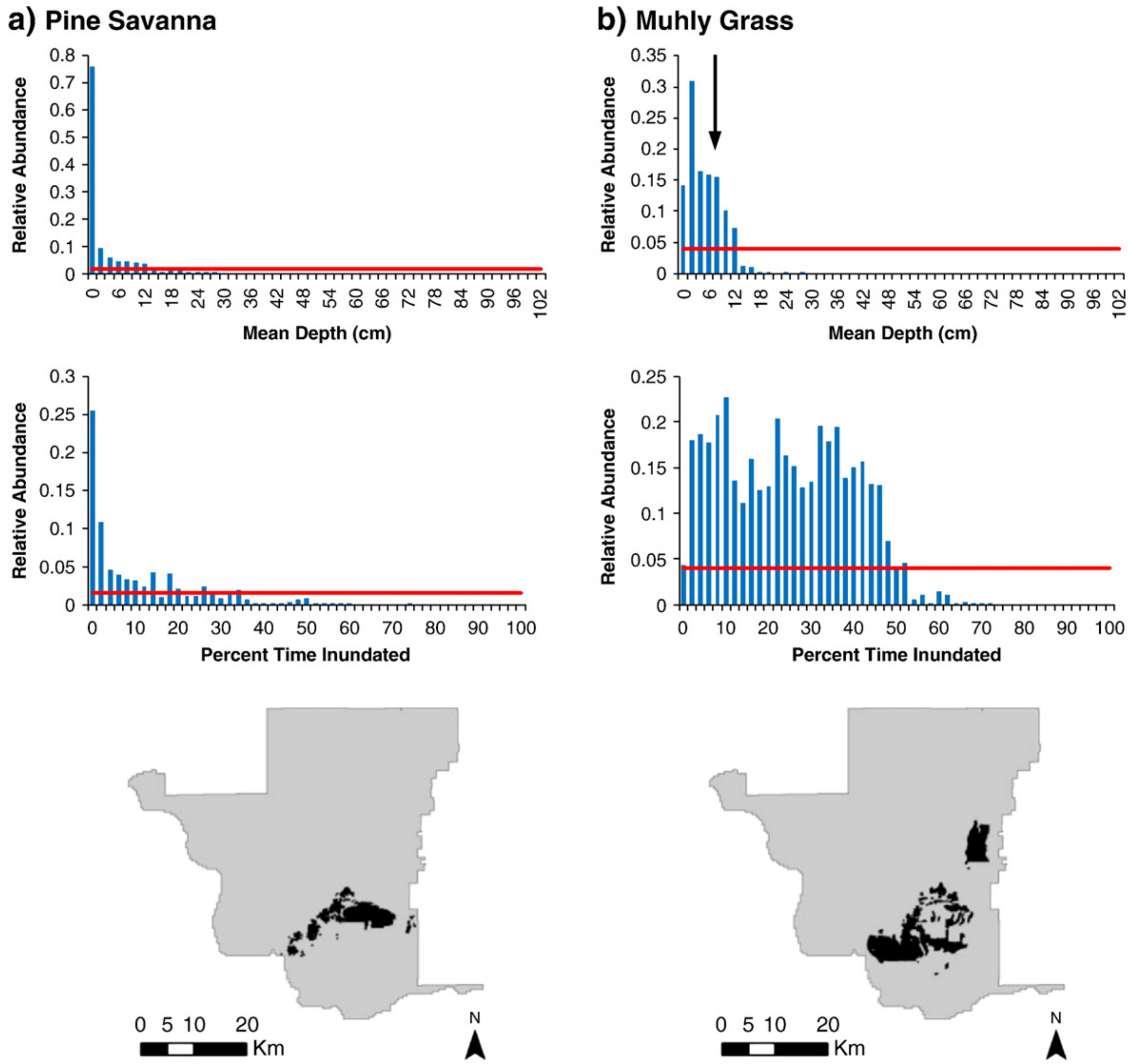

Fig. 6. (a) Pine savanna relative abundance for mean depth, relative abundance for percent time inundated, and spatial distribution. (b) Muhly grass relative abundance for mean depth, relative abundance for percent time inundated, and spatial distribution. The black arrow in b identifies the relative abundance calculation outlined in Section 2.4. The red line indicates the relative abundance of the given vegetation community across the entire landscape.

"Open Water"), thereby leaving 52 vegetation communities. Of these community types, sawgrass is the most abundant by an order of magnitude over any other vegetation type, totaling 66.5% of all pixels when sawgrass and tall sawgrass are combined (Table 1). A total of 13 vegetation types individually make up more than 1% of the total landscape (Table 1), with one of those being an exotic (Brazilian Pepper, *Schinus terebinthifolius*). Cumulatively these 13 types make up 92.2% of the total vegetation cover for the ENP landscape. We limited our analysis to those vegetation types constituting more than 1% of the landscape as it was difficult to develop dependable relationships between those types and their associated hydrologic characteristics due to small sample sizes.

Combining the hydrological and vegetation datasets, we investigated the differentiation of vegetation communities based on the hydrologic measures listed above. Plotting the distribution of a vegetation type for a particular hydrologic measure allowed us to identify areas where that community is disproportionately represented. For instance, pine savanna[1] (*Pinus elliottii* var. *densa*) constituted 1.6% of the total landscape, but was found predominantly at sites that were rarely flooded as its relative abundances at mean depths less than 20 cm and percent time inundated less than 20% are much higher than its system wide frequency (Fig. 6a). Additionally, it was not found beyond an average depth of 30 cm and makes up 76% of all pixels across ENP with a mean depth between 0 and 2 cm. These are reflected by its relatively high values of SI's: 6.6 and 2.4 for the mean depth and percent time inundated, respectively (Table 2). Note that when considering whether a SI value is 'high' or 'low', it should be placed in relation to the SI values of other vegetation communities in the system within the same hydrologic measure (see Table 2). Similarly, muhly grass (*Muhlenbergia filipes*) was predominant at more xeric habitats and rarely found above mean depths of 14 cm and percent time inundated of 54% (Fig. 6b). The SI values of muhly grass are 1.5 and 2.1 for the mean depth and percent time inundated, respectively (Table 2).

Our data were able to also discriminate vegetation communities frequenting the more hydric end of the hydrologic spectrum. Red mangrove scrub[2] (*Rhizophora mangle*) constituted 2.2% of ENP's landscape, but was found at higher relative abundances as compared

[1] Savanna is defined as a "low-density (open canopy) trees in a matrix of graminoids" [33].

[2] Scrub is defined as "Low-density areas of trees and shrubs with heights under 5 m" [33].

Table 2
Selectivity index (SI) for vegetation types related to hydrologic measure within Everglades National Park.

Vegetation type	Hydro	Depth	Duration	Percent wet
Sawgrass	**0.60**	**0.72**	**0.37**	**0.19**
Mixed gramminoids	0.82	1.14	1.18	1.01
Tall sawgrass	3.77	1.17	1.51	0.79
Muhly grass	1.12	1.53	1.03	**2.14**
Spike rush	1.36	1.76	2.00	0.93
Red mangrove scrub	**5.52**	**5.37**	**3.97**	1.14
Bayhead	1.90	0.78	0.74	0.59
Pine savanna	**15.2**	**6.58**	1.06	**2.44**
Willow shrublands	0.82	0.81	0.70	0.82
Dwarf cypress	0.96	1.18	0.91	1.47
Bay-hardwood scrub	**4.50**	**4.28**	**2.80**	1.15
Brazilian pepper	1.31	1.08	1.04	**2.08**
Cattail marsh	2.39	1.27	**5.20**	0.94

Only those vegetation types constituting more than 1% of the total landscape are listed.
Notes: Hydro, number of hydroperiods per year; Depth, conditional mean depth; Duration, mean duration of a hydroperiod; Percent wet, percentage of time inundated. The grey shaded cells represent the lowest SI while the green shaded cells represent the three highest SI for each hydrologic measure.

to its system wide frequency at depths greater than 36 cm and percent time inundated greater than approximately 80% (Fig. 7a). Its SI values are 5.4 and 1.1 for the mean depth and percent time inundated, respectively (Table 2). Similarly, the bay-hardwood scrub[3] community was found at higher than system wide relative abundances between approximately 20–80 cm mean depth and above 80% time inundated hydroperiod depth (Fig. 7b); its SI values are 4.3 and 1.1 for the mean depth and percent time inundated, respectively (Table 2).

Finally, plotting these histograms allows for the identification of vegetation types that exhibit less selection or are able to tolerate a very wide variety of hydrologic conditions. For instance, sawgrass is found across a range of individual hydrologic measures and at levels consistent with its distribution on the landscape (Fig. 8). This is reflected by its low SI values: 0.7 and 0.2 for the mean depth and percent time inundated, respectively (Table 2). Additionally, while sawgrass is by an order of magnitude the most common vegetation community found within ENP, the spatial distribution map of sawgrass (Fig. 8) makes it appear omnipresent across many portions of the map. This appearance is a result of the scale of the map, which causes the large number of pixels where sawgrass is the dominant vegetation type to overlap. However, if one looks at a more local spatial scale, while sawgrass still makes up a majority of the landscape, there are pixels where other vegetation types are represented (Fig. 9).

4. Discussion

Our results support the contention that many vegetation communities within the ENP are structured on hydrological gradients [2,27,29]. While multiple factors are undoubtedly important in determining the presence of a particular vegetation type at a given spatial location in a diverse and dynamic landscape such as the Everglades, our results decidedly show that hydrological processes are a major influence with the percent time inundated and the mean depth during that inundation being meaningful discriminatory variables. These findings support those of Gunderson [17] who suggests that duration and depth of flooding are the controlling variables on plant distribution within the Everglades ecosystem. Additionally, Zweig and Kitchens [38] showed that hydrology, and principally water depth, was the primary mechanism in driving vegetation community change in the Everglades ecosystem. However, the timescale of hydrologic influence on vegetation communities depended on community state. This study is one of the first to link vegetation distribution and hydrological processes at the large spatial scale of the entire ENP as most previous studies have attempted to relate hydrologic condition and vegetation community at the scale of a few meters to a few kilometers. This study takes a 7.75 year hydrologic record and uses mean values of calculated hydrologic measures to link the hydrological characteristics of the ENP to vegetation distribution. We argue that this study provides a wider, ecosystem level context of the relationship of hydrological processes to vegetation community distribution within the ENP.

The joint probability surface for percent time inundated and mean depth displays a positive correlation between increasing percent time inundated and mean depth (Fig. 5). At extremes of percent time inundated there is a wide range of mean depths, while over intermediate values of percent time inundated the range in depths is relatively narrow. The wider range in depths at either extreme of percent time inundated is not surprising as percent time inundated is bounded by those extremes (i.e. you cannot have less than 0% or more than 100% inundation). For instance, at the upper bound of inundation, a location cannot keep increasing its percent inundation so a wide of range of mean depths accumulate in these bins. Accordingly, at these extremes of percent time inundated, the mean depth may gain additional discriminatory power. The joint probability surface allows for the identification of those areas of percent inundation and mean depth that are most likely to occur together in the ENP. Correspondingly, the most likely inundation scenarios across the ENP range from 80 to 100% inundation and depths of 20–40 cm.

One could argue that the vegetation dataset used in this analysis represents a one-time snapshot of the vegetative landscape of the ENP and may not accurately represent current conditions. It is undoubtedly true that the vegetation community in some locations could have changed, but the time scale of vegetation change in relation to hydrologic change is one of much debate (see Introduction). This dataset represents the only known high-resolution vegetation map of the entire ENP and mapping of community type within this dataset represents the dominant vegetation community found at a location, not a census on every community present, thereby limiting the chance of a change. Combined with the large sample size (>5,000,000 pixels) and the fact that we are relating this vegetation type to a mean hydrologic condition over a long period of record (~8 years), we believe this analysis gives a good representation of the linkages between vegetation and hydrological processes across the entire ENP. This study also lays out a procedure for more detailed studies consisting of changing vegetation distribution and longer hydrologic data record periods.

Graphing of vegetation relative abundance in various hydrologic conditions (Figs. 6–8), characterized by the four measures listed above (Section 2.2), allowed us to discriminate differences among vegetation type. Sawgrass is by an order of magnitude the most abundant vegetation type within ENP (Table 1). By using mean depth and percent time inundated as hydrologic cues we are able to determine that sawgrass is found across a wide range of mean depths and percent times inundated, supporting findings in earlier studies [7,17,21,22]. This is especially evident in the graph of percent time inundated (Fig. 8), as sawgrass is found across all bins and not significantly different than found on average across the entire landscape, indicating that it can tolerate a wide range of inundation periods from quite dry to very wet. The graph of mean depth (Fig. 8) supports previous studies that suggest that the distribution of

[3] Bay-Hardwood Scrub is defined as "Mixed association of bayhead swamp species, buttonwood scrub and hardwood scrub species such as *Myrica cerifera*, *Chyrsobalanus icaco*, leather fern (*Acrostichum danaeifolium*), *Conocarpus erectus* and *Cladium jamaicense*. Minor species include *Metopium toxiferum, Ilex cassine, Persea borbonia, Sabal palmetto* and *Cephalanthus occidentalis*. Occurs in the transition zone between saline and fresh environments" [33].

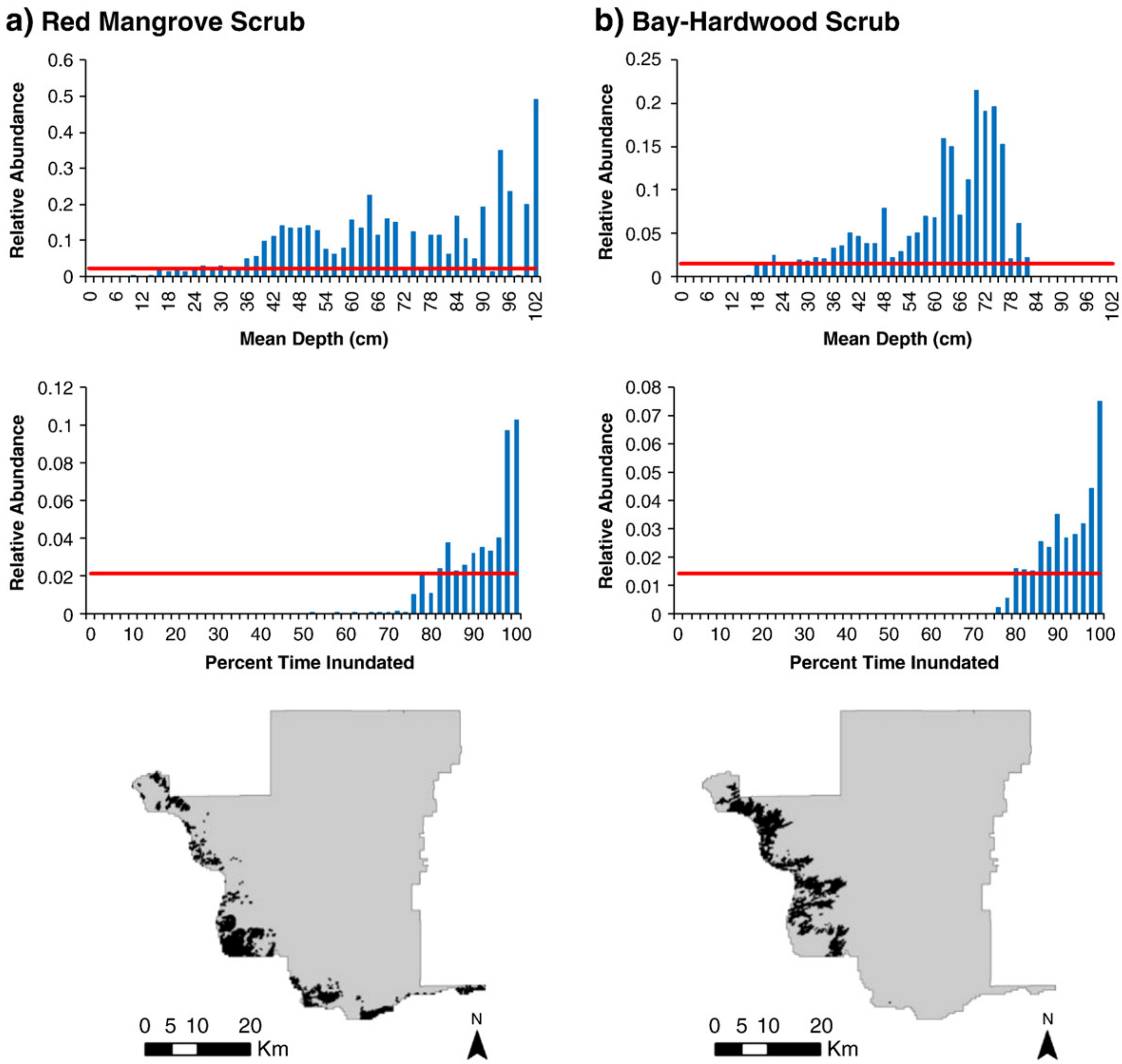

Fig. 7. (a) Red mangrove scrub relative abundance for mean depth, relative abundance for percent time inundated, and spatial distribution. (b) Bay-hardwood scrub relative abundance for mean depth, relative abundance for percent time inundated, and spatial distribution. The red line indicates the relative abundance of the given vegetation community across the entire landscape.

sawgrass is sensitive to the depth of inundation, but not the percentage of time inundated [1,17,22]. Fig. 8 shows that while sawgrass is found across all bins of mean depth, it is found much more frequently at locations with mean depths between approximately 10–40 cm and quite infrequently at deeper depths. This is consistent with previous researchers who found that sawgrass tends to prefer shallower conditions [4,6,27,29].

While the histograms of sawgrass suggested that it has adapted to survive at a variety of hydrologic conditions, this study supports the contention that other vegetation types are not. For instance, pine savanna (Fig. 6a) and muhly grass (Fig. 6b) are both found to favor relatively dry conditions as both have relative abundances above their system wide frequency at more shallow mean depths and lower time inundated percentages. The histograms of both pine savanna and muhly grass suggest they have physiological limits due to both mean depth and percent time inundated thereby limiting their presence at particular depths and percent times inundated. Recall that the vegetation dataset used in this study is based on identifying the "dominant" vegetation type. Therefore, while across a hydrologic measure we cannot ascertain the absolute presence or absence of an individual member of pine savanna or muhly grass, our data suggest that beyond certain hydrological limits these two vegetation types are outcompeted in favor of other more "dominant" types. For pine savanna, those limits appear to be 30 cm mean depth and 34% time inundated as its relative abundance decreases markedly beyond those values. For muhly grass, the corresponding thresholds appear to be beyond approximately 14 cm mean depth and 54% time inundated. These findings support those of Armentano et al. [2] who found that study sites originally dominated by muhly grass were replaced by sawgrass under increased inundation and longer hydroperiods, suggesting muhly grass prefers more xeric habitats while also corroborating the ability of sawgrass to survive under a wider range of hydrologic conditions.

In contrast, both red mangrove scrub (Fig. 7a) and bay-hardwood scrub (Fig. 7b) were found in areas with deeper mean depths and longer percent time inundated. The histograms of relative abundance for both of these vegetation communities suggest they are competitively more successful in more hydric environments across the ENP. For instance, red mangrove relative abundance is greater than its system wide abundance at mean depths greater than 36 cm and percent time inundated more than 84%. Bay-hardwood scrub is found predominantly at percent time inundated above 80%, but appears to

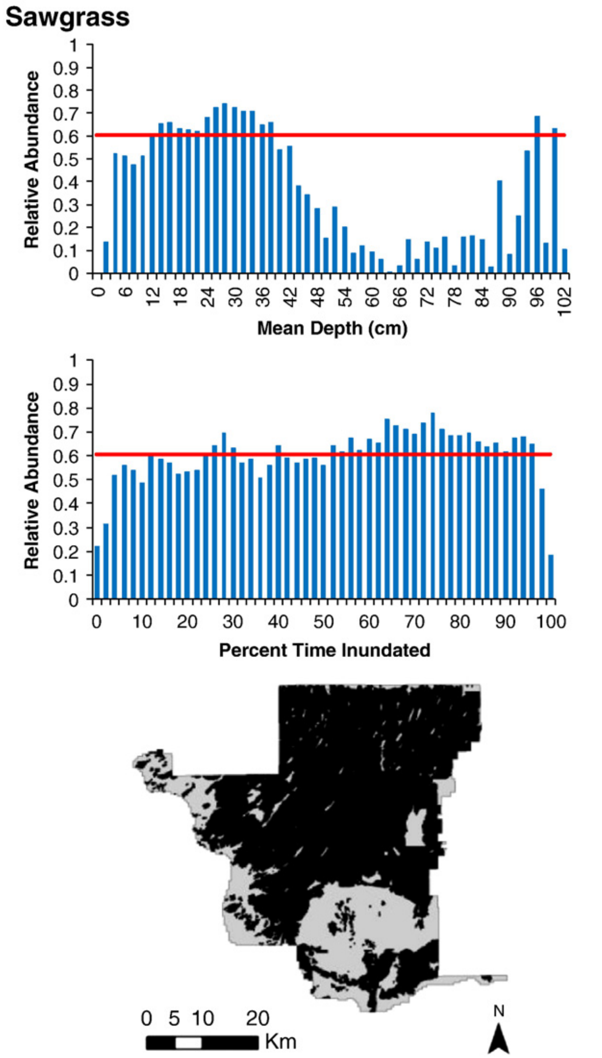

Fig. 8. Sawgrass relative abundance for mean depth, relative abundance for percent time inundated, and spatial distribution. The red line indicates the relative abundance of sawgrass across the entire landscape.

show a limit at both extremes of depth where it is absent at very shallow and very deep mean depths. This indicates that while bay-hardwood scrub prefers hydric habitats, there is a limit to the level of flooding it can tolerate.

While the histograms of individual plant community types to hydrologic measures support the structuring of these types along hydrologic gradients, this methodology does not readily lend itself for direct, quantitative comparison among vegetation types. Additionally, it offers few definitive results beyond observing that a vegetation type is more or less common than its system wide relative abundance for a given hydrologic measure. Here we couple graphical evidence of the histograms with a measure of the selectivity of a vegetation community type in an attempt to quantitatively identify those communities most influenced by their surrounding hydrologic characteristics (Table 2). The measure of a SI in this study helped elucidate those communities with different degrees of hydrological preference. The SI's based on the four hydrologic measures were calculated for all community types constituting more than 1% of the ENP landscape. For all four hydrologic measures, sawgrass had the lowest SI (Table 2), thereby reinforcing the graphical evidence (Fig. 8) of it being able to survive a wide variety of hydrologic conditions. The measurement of SI also helped identify those community types considered more "selective". Pine savanna (Fig. 6a), red mangrove scrub (Fig. 7a), and bay-hardwood scrub (Fig. 7b) all ranked in the top three highest values of SI for three out of the four measured hydrologic measures indicating they may be structured by multiple hydrologic variables (Table 2) relative to other vegetation community types. Additionally, these three vegetation community types had the highest average SI for the two measures focused on in this paper, namely percent time inundated and mean depth. Sawgrass was once again lowest. Meanwhile, a community type like muhly grass (Fig. 5b) or cattail marsh was in the top three values of SI in percent time inundated and duration respectively, indicating their distribution may be determined by a single hydrologic measure.

Investigations on the importance and dependence of scale in discerning spatial patterns has been of growing importance in the last several decades with a general consensus that there is no single correct scale to characterize landscape heterogeneity [35,36]. As such, we recognize that the databases used in this study are influenced by their scale and the results and conclusions presented in this paper could be scale-dependent. Nonetheless, several reasons lend support to their significance and robustness. For instance, within the Everglades ecosystem, multiple studies have looked at the appropriate spatial scale of studying ecosystem dynamics. For example,

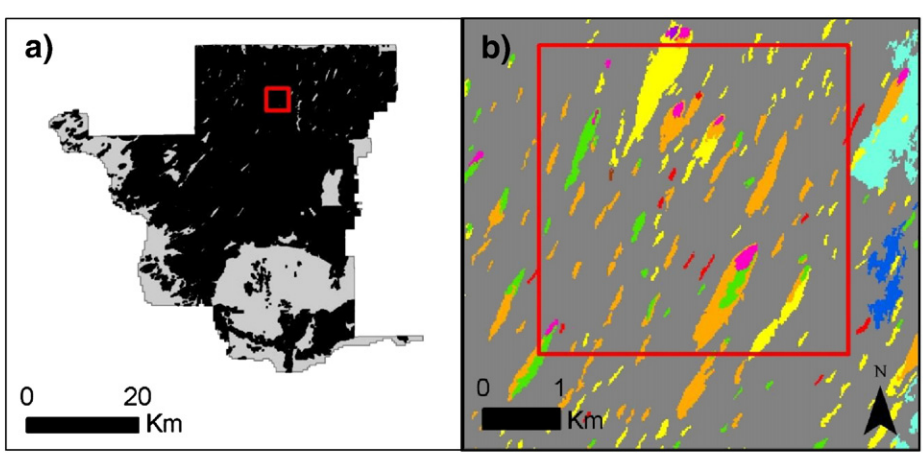

Fig. 9. (a) Sawgrass spatial distribution with selected area and (b) inset showing dominant vegetation type within selected area. Grey in (b) represents sawgrass. Other vegetation types include: tall sawgrass (yellow), willow (orange), bayhead (green), graminoid prairie/marsh (light blue), open water (blue), subtropical hardwood forest (pink), hardwood scrub (red), cattail (brown), and non graminoid emergent marsh (purple).

Obeysekera and Rutchey [26] showed that a pixel resolution of 100 m may be the upper limit for ensuring patch characteristics in landscape models, while Rutchey and Godin [30] proposed a minimum mapping unit resolution of 50×50 m for vegetation. Our vegetation dataset is at a finer spatial scale than the recommended minimum mapping unit suggested by these previous studies.

Importantly, by focusing on only those vegetation types with large spatial extents, from cattail marsh (57,519 pixels) to sawgrass (3,210,402 pixels) (Table 1), our results are expected to be statistically significant. That is, while the "true" hydrological features experienced by scale may differ from those extracted from EDEN at the 400×400 m scale, this discrepancy would likely have small effects on the overall behaviors or patterns statistically inferred from tens of thousands of pixels such as those in Figs. 4–8. Furthermore, the EDEN dataset has been shown to be accurate in multiple validation studies, even at smaller scales [13,24]. These suggest that the issue of scale dependence, while undoubtedly affecting some quantitative details, does not strongly affect our general conclusions regarding the hydrological preference of the Everglades vegetation. All in all, we argue that this analysis represents a positive first step at relating hydrological processes to vegetation community distribution across the entire ENP and at the same time support revalidation of these results as longer term and greater resolution datasets become available. Additionally, findings from this study will benefit the development of more process-based or physiologically based models, which will offer additional insights and predictive capability in relating vegetation communities to their surrounding hydrologic characteristics.

Everglades National Park is a vast, highly diverse landscape with numerous vegetative communities subject to a multitude of hydrologic conditions. This work is among the first to show hydrologic structuring of vegetation communities at the ecosystem scale across the entire ENP via analysis of a location's mean depth and percent time inundated. By comparing a vegetation community's relative abundance at given depths and percent times inundated relative to its system wide abundance, we have shown that vegetation communities react differently to hydrologic conditions. A community like sawgrass is able to persist in a variety of hydrologic conditions while the distribution of a community like pine savanna or bay-hardwood scrub is more narrow and controlled by their hydrologic environment. This paper was focused on showing the link of hydrological characteristics to vegetation community distribution at a large spatial scale, but the ENP is a landscape under growing threat from increased human alteration and climate change. Based on our findings, changes in the hydrology within ENP can potentially have profound impacts on the distribution and prevalence of the vegetation communities and is the subject of ongoing work.

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