FRESHWATER ECOLOGY

Long-term nutrient enrichment, mowing, and ditch drainage interact in the dynamics of a wetland plant community

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Abstract. Fertilization studies have elucidated basic principles of the role of nutrients in shaping plant communities and demonstrated the potential effects of anthropogenic nutrient deposition. Yet less is known about how these effects are mediated by interacting ecological factors, particularly in nutrient-poor wetland habitats. In a long-term experiment in a coastal plain wetland, we examined how fertilization and mowing affected the diversity and composition of a plant community as it reestablished after major disturbance. A drainage ditch in proximity to the experimental plots allowed us also to consider the influence of hydrology and its interactions with nutrient addition. Fertilization decreased species richness, with wetland specialist species showing especially great losses, and several lines of evidence suggest that the effect was mediated by competition for light. Altered hydrology via ditch drainage had effects that were similar to fertilization, with more rapidly draining plots showing lower diversity and decreased abundance of wetland species. Plant community diversity and dynamics were influenced by complex interactions between fertilization, disturbance, and hydrology. The negative effect of fertilization on species richness was initially mitigated by mowing, but in later years was more evident in mowed than in unmowed plots. In the absence of disturbance, nutrient addition increased the rate of transition to primarily woody communities. Similarly, drained plots experienced increased rates of succession compared to wetter plots. Our results suggest that these interactions need to be considered to understand the potential effects of anthropogenic nutrient addition and hydrologic alterations to wetland ecosystems.

Key words: disturbance; ditch; diversity; fertilization; hydrology; mowing; nutrient addition; nutrient enrichment; plant community; species richness; succession; wetland.

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INTRODUCTION

Industrial processes, agricultural activities, and combustion are estimated to contribute substantially to atmospheric phosphorus and fixed nitrogen, resulting in dramatically increased deposition rates since pre-industrial times (Mahowald et al. 2008, Wang et al. 2015, Jia et al. 2016). Given current and projected levels of anthropogenic nutrient addition, interest centers on understanding its consequences for natural communities (Krupa 2003, Stevens et al. 2004, Gilliam 2006, Phoenix et al. 2006, Clark and Tilman 2008, Bobbink et al. 2010). Thus, basic knowledge of how nutrient availability shapes plant communities has particular relevance in the Anthropocene. While a large literature of fertilization studies has elucidated key principles, less is known about how the effects of nutrient inputs are mediated by interacting ecological factors that characterize

natural landscapes, particularly in isolated, nutrient-poor wetland habitats.

Classic nutrient addition experiments, primarily focused on grassland communities, have generally found that fertilization decreases species diversity (Silvertown et al. 2006, reviewed in DiTommaso and Aarssen 1989, Gough et al. 2000, Suding et al. 2005, Clark et al. 2007). Mechanisms proposed to explain the loss of diversity with higher nutrient availability include loss of rare species caused by reduced plant densities as biomass of individual plants increases (Oksanen 1996), reduced niche dimensionality (Harpole et al. 2016, 2017), and alterations to competitive interactions. In a leading competition-based explanation, addition of nutrients is hypothesized to result in a shift from belowground to aboveground competition for a single resource—light (Newman 1973). As productivity increases with nutrient availability, competitive exclusion by species best able to access light drives diversity downward (Goldberg and Miller 1990, Borer et al. 2014) and can cause dramatic shifts in plant community composition.

Although consistent trends emerge from fertilization studies, the results can vary temporally (Hooper and Johnson 1999, Waring et al. 2019) and among plant community types (Gough et al. 2000), reflecting the impacts of other ecological variables that influence community responses to nutrients. For example, in an analysis of 23 N-addition experiments, the magnitude of species loss varied across study sites and was strongly influenced by regional climate and soil properties (Clark et al. 2007). The effects of nutrient levels on competitive interactions may depend on the availability of other limiting resources. Similarly, the magnitude of response to nutrient addition also depends on light availability (Borer et al. 2014), which is affected by herbivory and disturbance. Such environmental variation complicates predictions of how experimental fertilization or anthropogenic nutrient enrichment will affect natural communities. However, few fertilization studies have simultaneously manipulated other factors that modify nutrient effects on plant communities (Britton and Fisher 2007, Hautier et al. 2018).

Hydrology, which is often altered by human activities, also has demonstrated effects on plant community composition. Studies of both naturally existing and manipulated gradients have revealed associations between hydrology and plant community composition and diversity (Lu et al. 2009, Fraaije et al. 2015, Oddershede et al. 2018). Soils of wetlands are often nutrient-poor and support slow-growing species adapted to conditions of low nutrients and frequently inundation (Keddy 1990, Aerts and Chapin 1999). Increased nutrient availability in wetlands can facilitate the encroachment of invasive and generalist species, causing shifts in community structure (Pauli et al. 2002, Perry et al. 2004). Because of the links between soil moisture, soil fertility, and plant community composition, the effects of nutrient enrichment might be influenced by hydrological conditions, yet these interactions have received relatively little study (Gasarch and Seastedt 2015).

In a 14-yr manipulative experiment, we quantified the effects of fertilization and disturbance on the diversity and composition of a wetland plant community on the coastal plain of North America. Infertile coastal plain wetlands provide a unique opportunity for examining the effects of fertilization on diversity because they are characterized by high diversity of rare species (Moore et al. 1989, Keddy, 1994, Noss et al. 2015), and the southeast U.S. coastal plain region experiences unusually high rates of atmospheric nutrient deposition (National Atmospheric Deposition Program 2019). Therefore, studies of nutrient addition in the coastal plain region are critical for understanding how ongoing environmental change and nutrient deposition influences functionally important wetland ecosystems. Here, we explore the effects of experimental nutrient addition and mowing in a full-factorial design. A drainage ditch positioned along one side of the experimental plot also created a hydrological gradient that allowed us to investigate how hydroperiod interacts with nutrient addition in a wetland habitat. We discuss the relative strength of the effects of these factors and the importance of considering how complex interactions among ecological variables influence plant community patterns.

Methods

Study site

The long-term experiment is located within East Carolina University's West Research

Campus, a tract of land in the North Carolina coastal plain with elevations of 22–25 m. The flat topography causes poor drainage, and over 60% of the tract has been classified as jurisdictional wetlands. Soils are acidic and poorly drained (Chester 2004) with generally low fertility (see Appendix S1: Table S1), consistent with the presence of several carnivorous plant species. Comparisons to reference floras indicate a diverse mosaic of plant community types: wet pine flatwood, pine savanna, and mixed hardwood (Chester 2004). The presence of fire-adapted plant species suggests that the site experienced frequent wildfires in pre-settlement times. For several decades preceding the experiment, the tract was maintained as an open landscape by a combination a mowing and prescribed burns. In 2002, the experiment was established on a 0.7-ha plot.

Experimental design

To prepare for installation of the experiment in 2003, the area was mowed, burned, and tilled. Since 2004, we have documented the development of the plant community in the experimental treatment plots. Taxonomy follows the PLANTS Database (USDA and NRCS 2019); taxonomic authorities can be found there. Treatments are replicated on eight 20 × 30 m blocks arranged in two rows of four (Fig. 1). Mowing (disturbance) and fertilization (nutrient addition) are applied in a full-factorial randomized block design to yield four treatment plots per block: (1) no mowing, no fertilizer; (2) no mowing, fertilizer; (3) mowing, no fertilizer; and (4) mowing, fertilizer. Pellet fertilizer (10-10-10 NPK) is applied three times per year to achieve an annual supplementation rate of 45.4 kg/ha for each nutrient. Aboveground vegetation in mowed plots is removed in early winter by a tractor-pulled rotary mower and raked afterward to more closely simulate the removal of litter by wildfire, historically a source of natural disturbance in this region. A roadside drainage ditch that lies along one row of blocks (Fig. 1) creates a hydrological gradient (Goodwillie and Franch 2006). Soil water content in the four blocks farther from the ditch, as measured by a capacitance meter (Extech MO750 soil moisture meter) in spring 2018, was more than two times that of four blocks adjacent to and presumably drained by the ditch ($F_{1,6} = 26.48$,

$P = 0.002$). Moreover, standing water is often present in blocks farther from the ditch but not in those adjacent to it, with the transition in pooling coinciding closely with the location of the near and far rows. Although soil moisture is also likely to show continuous variation, we treated it here as a categorical variable for simplicity of analysis.

Vegetation sampling

We sampled the plant community in three permanent, randomly placed 1-m^2 quadrats per plot. Quadrats were located at least 3 m from borders with adjacent plots or block edges to minimize confounding effects of fertilizer run-off or shading by unmowed plots. Plant community data for the 96 quadrats (8 blocks × 4 treatment plots × 3 quadrats) were collected each August from 2004 to 2017, except for 2012 and 2014, recording stem count and percent cover of each species. To quantify abundance, species importance values were calculated for quadrats as the sum of relative density (number of stems/total stems of all species) and relative cover (percent cover/sum of percent cover of all species).

Analysis of plant community data

We ran generalized linear mixed models (GLMMs) using package glmmTMB (Brooks et al. 2017), in the R statistical programming environment (R Core Team 2018) and used the packages effects (Fox 2003), DHARMa (Hartig 2019), car (Fox and Weisberg 2019), bbmle (Bolker and R Development Core Team 2017), aods3 (Lesnoff and Lancelot 2018), broom (Robinson and Hayes 2019), ggplot2 (Wickham 2016), and gridExtra (Auguie 2017) to conduct model diagnostics, extract relevant statistical summaries, and generate graphical summaries. Specifically, we tested for the fully crossed effects of mowing, fertilization, year, and proximity to a drainage ditch on (1) the overall species richness and (2) the proportional abundance of wetland specialist species using separate GLMMs. For diversity analysis, we focus only on species richness here because analyses of the Shannon diversity and Simpson's evenness indices gave qualitatively similar results. In each model, mowing, fertilization, and ditch proximity were included as categorical fixed effects and year was incorporated as a continuous fixed effect. To
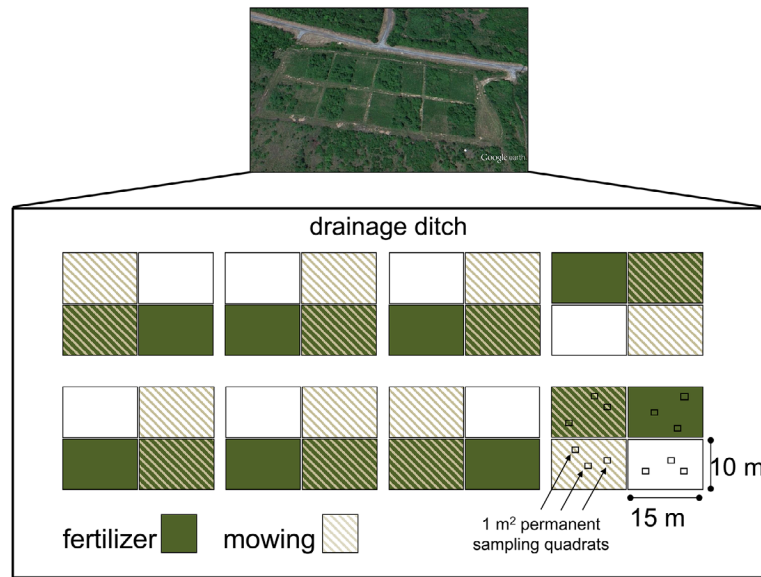
Fig. 1. Schematic of experimental design. Treatments (fertilizer/no fertilizer, mowing/no mowing) were assigned randomly to one or the other side of each block replicate. Plant community data are sampled at three permanently marked 1-m² quadrats (shown only for one block).

account for potential spatial autocorrelation from repeated sampling of the same quadrats, we included quadrats nested within experimental blocks nested in proximity to ditch as a three-level nested random effect in the models. For analysis of species richness, we assumed a log-normal error distribution and assumed beta errors for analyses of relative abundance. Proportional abundances of wetland specialist species were obtained by summing the importance values for all species with obligate wetland status in the southeastern U.S. region (USDA and NRCS 2019), defined as species that almost always occur in wetlands. However, because there were no obligate wetland species at some sites to meet the assumption of the beta regression model, we rescaled the data to lie in the interval between 0 and 1. The function,

$$y' = (y - a)/(b - a)$$

can be used to rescale data with known bounds (*a, b*)into the unit interval between *a* and *b* without loss of generality (Smithson and Verkuilen 2006). Model diagnostics were conducted based on visual inspection of residuals, conditional modes, and QQ plots where appropriate. Statistical inferences for fixed effects were calculated

from type II analysis of variance tables whereby Wald chi-squared statistics are calculated following the principle of marginality (Fox and Weisberg 2019).

We ran multivariate analyses to examine among-treatment differences in the composition of plant communities. We used the adonis function in the vegan package (Oksanen et al. 2018) to perform permutational multivariate analysis of variance (PERMANOVA). Bray-Curtis dissimilarities were calculated from species importance values for each quadrat. For this analysis, we implemented the same model used for the univariate analyses, in which mowing, fertilizer, and year were included as fully crossed fixed effects, ditch as an additive fixed effect, and quadrat nested within block as a nested random effect. To visualize the community responses to treatments, ditch proximity, and year, we used principal coordinates analysis (PCoA) of the normalized plant community matrix based on the Bray-Curtis dissimilarity. For the most recent data only (2017), we ran the Dufrene-Legendre Indicator Species Analysis (Dufrêne and Legendre 1997) to identify plant species that were most representative in each of the eight treatment combinations (two levels of mowing × two

levels of fertilization × two levels of ditch proximity). This was conducted using the indval function of the labdsv package (Roberts 2016).

Biomass

Aboveground plant biomass was quantified in mowed and mowed/fertilized plots at the end of the growing season in 2010 and 2017 by clipping all plants in a 0.25-m^2 area at ground level, drying them at 60°C for 48 h, and weighing the plant tissue. The method was not feasible for unmowed plots because they contained large trees. We collected biomass data at three randomly chosen locations per plot for a total of 48 samples (8 blocks × 2 treatments × 3 samples). We used a GLMM assuming a log-normal error distribution to analyze the fully crossed effects of fertilization, year, and proximity to the drainage ditch on the overall biomass of plants in the mowed plots.

RESULTS

Plant community analyses

Species richness was affected by fertilization, mowing, and proximity to the ditch (Table 1, Fig. 2) and declined through time in all treatments (year: Wald X^2 = 479.36, P < 0.001). Fertilization reduced species richness, causing steeper rates of decline (fertilizer × year: Wald X^2 = 20.92, P < 0.001). In contrast, mowing reduced the rate of decline in diversity (mowing × year: Wald X^2 = 171.92, P < 0.001). The effect of fertilizer on species richness was generally greater in mowed than in unmowed plots, but the interaction effect varied through time (fertilization × mowing × year: Wald X^2 = 5.14, P < 0.023). Plots close to the drainage ditch had ~19% fewer species than more distant, wetter plots (ditch effect: Wald X^2 = 42.35, P < 0.001), and the ditch interacted with other treatments to influence species richness (e.g., ditch × fertilizer × mowing × year: Wald X^2 = 6.09, P = 0.014).

The proportional abundance of wetland species has also declined over time, with steeper losses in unmowed than in mowed plots (Fig. 3, mowing × year: Wald X^2 = 15.55, P < 0.001). As with species richness, negative effects of fertilization on wetland species through time were stronger in mowed than in unmowed plots (fertilizer × mowing × year: X^2 = 9.64, P = 0.002). Ditch proximity had a strongly negative influence on the abundance of wetland plants: Proportional abundance was ~ 70% lower in plots close to the ditch (ditch effect: Wald X^2 = 17.20, P < 0.001). The magnitude of the ditch effect was greatest in

Table 1. Effects of experimental factors on plant species richness and relative abundance of wetland species.

Source of variation	df	Species richness		Wetland species relative abundance†	
		X^2	P‡	X^2	P‡
Fertilizer	1	51.328	<0.001	3.042	0.081
Mowing	1	147.851	<0.001	38.876	<0.001
Year	1	479.364	<0.001	99.109	<0.001
Ditch	1	42.352	<0.001	17.196	<0.001
Fertilizer × Mowing	1	2.675	0.102	12.003	<0.001
Fertilizer × Year	1	20.924	<0.001	1.677	0.195
Fertilizer × Ditch	1	0.118	0.732	3.034	0.082
Mowing × Year	1	171.915	<0.001	15.552	<0.001
Mowing × Ditch	1	0.445	0.505	8.698	0.003
Year × Ditch	1	11.159	<0.001	36.860	<0.001
Fertilizer × Mowing × Year	1	5.142	0.023	9.635	0.002
Fertilizer × Mowing × Ditch	1	0.502	0.479	14.040	<0.001
Fertilizer × Ditch × Year	1	3.529	0.060	1.126	0.289
Mowing × Ditch × Year	1	6.029	0.014	4.456	0.035
Fertilizer × Mowing × Ditch × Year	1	6.087	0.014	0.537	0.464

Note: Results of analysis of deviance.
† Abundance of wetland species was calculated as the sum of importance values of obligate wetland species, as defined in the USDA Plants Database.
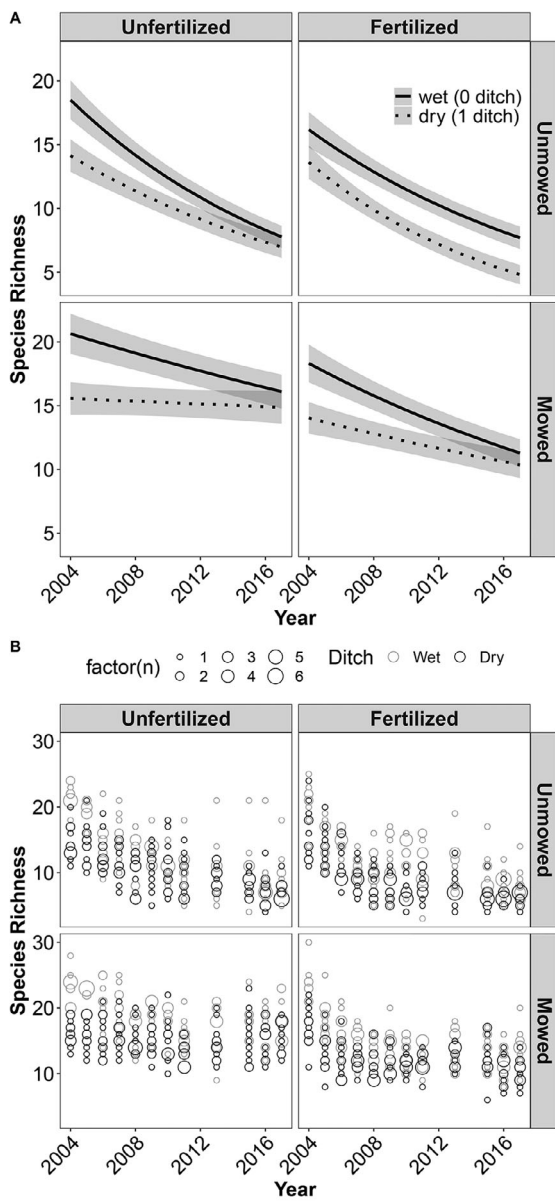‡ P-values determined by Wald chi-squared test.

Fig. 2. Species richness in treatment combinations through time. (A) Dashed lines indicate drier blocks adjacent to drainage ditch; solid lines indicate wetter blocks farther from drainage ditch (see Fig. 1). Shaded envelopes indicate 95% confidence region for the fitted line. (B) Raw quadrat data. Black circles indicate drier blocks adjacent to drainage ditch; gray circles indicate wetter blocks farther from drainage ditch. Size of circle (factor number) indicates the number of data points falling within each interval.

mowed/unfertilized plots because obligate wetland species have been greatly diminished by fertilization and succession (in unmowed plots) regardless of ditch proximity (fertilizer × mowing × ditch effect: Wald $X^2 = 14.04$, $P < 0.001$).

All main factors (fertilizer, mowing, year, ditch) and all two-, three-, and four-way interactions influenced plant community composition (Table 2). Based on main factor effects, mowing followed by year, ditch, and then fertilizer explained the most variation in plant community composition (mowing $R^2 = 0.100$, year $R^2 = 0.077$, ditch $R^2 = 0.065$, fertilizer $R^2 = 0.040$; Fig. 4, Table 2). Plant community composition in unmowed plots changed over time largely along PCoA axis 1, which likely corresponds to increased dominance of woody species. Both ditch proximity and fertilization caused communities to shift primarily along PCoA axis 2 (Fig. 4). Species indicator analysis for 2017 community data identified between one and ten indicator species per treatment combination, with significant indicator values ranging from 0.2 to 0.86 (Table 3). Most of the indicator species for unmowed plots were woody species (e.g., *Liquidambar styraciflua*, *Cyrilla racemiflora*). Obligate wetland indicator species (e.g., *Scleria minor*, *Solidago stricta*) were exclusively associated with wetter plots farther from the ditch.

Biomass

Aboveground biomass increased with fertilization, but the magnitude of the effect differed between two years of sampling (fertilizer × year: $X^2 = 30.59$, $P < 0.001$; Table 4, Fig. 5); fertilizer increased average biomass by only 16.5% in 2010 as compared to 96.7% in 2017. The difference in magnitude resulted from reduced biomass of unfertilized plots in 2017 (Fig. 5). Ditch proximity also had a significant effect on biomass production, with plots adjacent to the ditch showing 30.7% higher average biomass than plots farther from the ditch.

Discussion

The results of this long-term, multifactorial experiment in a coastal plain wetland highlight
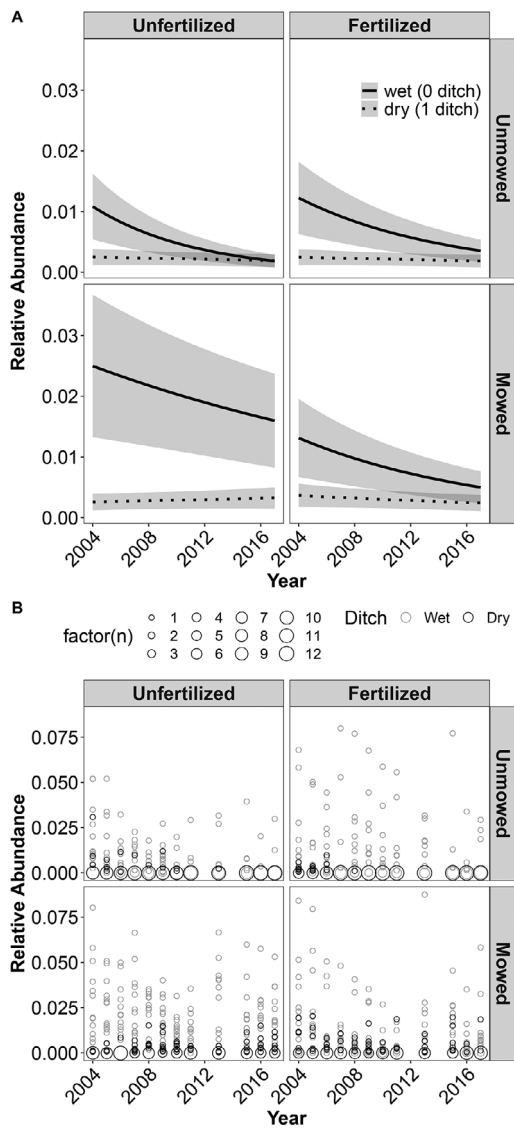
Fig. 3. Relative abundance of obligate wetland species in treatment combinations through time. Relative abundance calculated as the summed importance values of all obligate wetland species, as defined by Plants Database (USDA and NRCS 2019) for the southeastern United States. (A) Shaded envelopes indicate 95% confidence region for the fitted line. Dashed lines indicate drier blocks adjacent to drainage ditch; solid lines indicate wetter blocks farther from drainage ditch (see Fig. 1). (B) Raw quadrat data. Black circles indicate drier blocks adjacent to drainage ditch; gray circles indicate wetter blocks farther from drainage ditch. Size of circle (factor number) indicates the number of data points falling within each interval.

the complex interacting effects of nutrients, disturbance, and hydrology on plant community composition. The main effects of fertilization on diversity and species composition were generally consistent with expectations from previous empirical and theoretical studies; their interactions with disturbance and hydrology provided novel insights.

Nutrient addition effects on diversity

Congruent with many nutrient addition experiments (Silvertown et al. 2006, reviewed in DiTommaso and Aarssen 1989, Gough et al. 2000, Suding et al. 2005, Clark et al. 2007), fertilization resulted in an overall decline in species richness in our study. As seen in the strength of the main effect and fertilizer × year interaction, the addition of nutrients has caused steep declines; after 14 yr, the mean number of species per m^2 averaged across all fertilized plots (~8 species) is 26.3% lower than that of unfertilized plots. The magnitude of the effect in our study is comparable to the 30% mean reduction in species richness found in a meta-analysis of fertilization studies (Gough et al. 2000).

Competition for light has been proposed as a primary mechanism for the loss of diversity with nutrient enrichment. According to the light asymmetry hypothesis (Goldberg and Miller 1990, Hautier et al. 2009, Borer et al. 2014, DeMalach et al. 2016), high nutrient availability releases plant species from belowground competition for multiple nutrients, intensifying aboveground competition for light. Taller plants, receiving more light per unit biomass, outperform shorter ones ultimately resulting in competitive exclusion. Although we did not measure light levels in our study, combined evidence suggests a substantial role of competition for light in the loss of diversity with fertilization, especially in mowed plots.

First, the abundance of tall species showed particularly large increases with fertilization in mowed plots, which is expected to reduce light available to smaller species. Two of the tallest species in disturbed plots, switchcane (*Arundinaria tecta*) and winged sumac (*Rhus copallinum*), were indicator species for mowed/fertilized treatments, showing 79% and 135% greater abundance, respectively, in mowed/fertilized than in

Table 2. Effects of experimental factors on plant community composition.

Source of variation	df	Sum of squares	F model	R^2	P†
Fertilizer	1	12.45	74.79	0.040	<0.001
Mowing	1	30.83	185.21	0.100	<0.001
Year	1	23.88	143.48	0.077	<0.001
Ditch	1	19.93	119.72	0.065	<0.001
Fertilizer × Mowing	1	3.46	20.75	0.011	<0.001
Fertilizer × Year	1	2.23	13.38	0.007	<0.001
Fertilizer × Ditch	1	4.03	24.23	0.013	<0.001
Mowing × Year	1	7.21	43.30	0.023	<0.001
Mowing × Ditch	1	4.55	27.31	0.015	<0.001
Year × Ditch	1	5.28	31.71	0.017	<0.001
Fertilizer × Mowing × Year	1	1.01	6.07	0.003	<0.001
Fertilizer × Mowing × Ditch	1	2.65	15.91	0.009	<0.001
Fertilizer × Year × Ditch	1	0.55	3.28	0.002	0.002
Mowing × Year × Ditch	1	0.80	4.77	0.003	<0.001
Fertilizer × Mowing × Year × Ditch	1	0.32	1.94	0.001	0.035
Residuals	1,136	189.10		0.613	
Total	1,151	308.26		1.000	

Note: Adonis (PERMANOVA) results based on Bray-Curtis distances.
† *P*-values computed from 1000 permutations.

mowed plots. Moreover, a functional trait analysis in our experiment found that the community weighted mean for plant height was 42% greater in mowed/fertilized plots than in mowed plots (Tate 2018). Mean leaf size—another trait that facilitates competition for light (Douma et al. 2012)—was also greater in fertilized plots in our study (Tate 2018). Second, fertilization caused a near doubling in aboveground biomass in 2017, which is likely to have decreased the amount of light reaching the ground (Borer et al. 2014). However, in a global analysis, losses of diversity increased with the number of nutrients added even when biomass was controlled for (Harpole et al. 2016), indicating that the multidimensionality of nutrient resources can also contribute to maintaining diversity (Dickson and Foster 2011, Harpole et al. 2017). Because our study did not include factorial nutrient treatments, we could not address whether this mechanism is also acting on diversity.

Mowing effects and interactions

Disturbance by mowing played an essential role in maintaining diversity. Without mowing, the mean combined species richness of forbs and graminoids declined from ~14 to 2 species per m^2 during the 14-yr period. During that time, woody plant diversity rose only slightly from two to four species with the encroachment of slower-growing wetland species (e.g., *Cyrilla racemiflora* and *Symplocos tinctoria*) following the early domination of rapidly growing generalist trees (*Nyssa sylvatica* and *Liquidambar styraciflua*). Despite small gains in woody plant diversity, unmowed plots show dramatically lower species richness overall, consistent with other studies of wet meadow and grassland communities (Opdekamp et al. 2012, Pfeiffer et al. 2017).

As a caveat, the scale at which we measured species richness might have influenced comparisons of mowed and unmowed data. Because trees dominate the unmowed plots, the number of species that coexist in a 1-m^2 quadrat might be lower because of plant size (Oksanen 1996). Nevertheless, the total number of species present in 2017 in all unmowed quadrats combined (31) was less than half the total for mowed plots (65), suggesting that the effect detected in quadrat data is not caused solely by a sampling artifact.

Although lack of mowing and nutrient enrichment has exacerbated the loss of species richness, all treatment plots have experienced some reduction in diversity, which reflects in part the loss of small, short-lived species that colonized tilled soils at the start of the experiment. For example, in mowed/unfertilized plots, a small biennial forb (*Polygala lutea*), a short-lived perennial forb
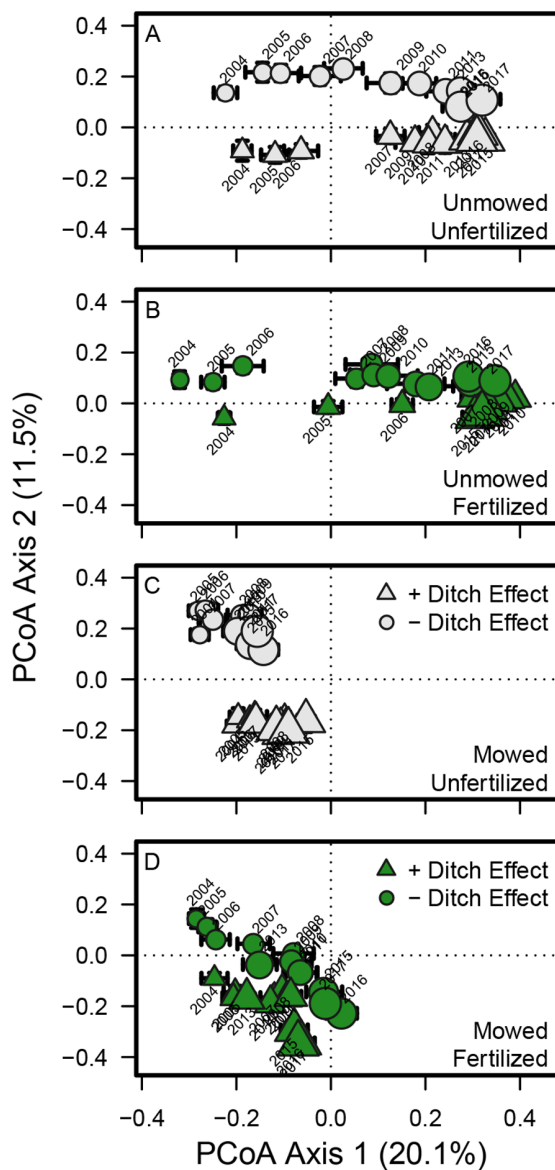
Fig. 4. Principle components analysis (PCoA) of plant community composition based on Bray-Curtis dissimilarity matrix of species importance data. All data were analyzed in a single PCoA, but results for different treatment combinations are shown in separate panels (A–D). Symbols indicate centroids for each year and treatment combination, and error bars indicate data range. Triangles represent plots adjacent to and drained by a ditch; circles represent wetter plots farther from the ditch. Size of symbols increases through progressive years (2004–2017).

(*Gratiola pilosa*), and an annual grass (*Amphicarpum purshii*) were common at the start of the experiment (mean stem count per m^2 = 1.5, 5.5 and 4.6, respectively) but were absent in 2017. In contrast to the initial tilling, annual mowing does not disrupt the formation of clumped, clonal species which may preclude seedling recruitment of non-clonal plants. While annuals and some small, non-rhizomatous perennials have been lost, *Solidago rugosa* and *Arundinaria tecta,* a strongly clonal forb and grass, have increased in abundance in mowed/unfertilized plots by 374% and 273%, respectively, since the start of the experiment.

Importantly, mowing and fertilization interacted to influence plant community diversity and composition, and the outcome has changed through time (fertilizer × mowing × year effect). In the first year, nutrient addition reduced plant diversity in unmowed but not in mowed plots (Goodwillie and Franch 2006), suggesting that biomass removal can mitigate the negative effects of eutrophication by limiting competition for light (Borer et al. 2014, Hautier et al. 2018, Yang et al. 2019). In 2017, however, the reduction in species richness with nutrient addition was nearly twice as great in mowed than in unmowed plots. This trend is consistent with light competition as a driver of species loss; with succession to a woody community, the understory of both fertilized and unfertilized unmowed plots has become uniformly light-limited such that nutrient availability has a less pronounced effect (Coomes and Grubb 2000, Neufeld and Young 2014). Nevertheless, fertilization has continued to have some impact on species richness in our tree-dominated plots, as seen in other forest communities (Gilliam 2006), suggesting that causal mechanisms other than light competition may also be acting.

Treatment effects on wetland species abundance

Proximity to a ditch has decreased species diversity by 19% overall, and the reduction stems largely from the negative effects on wetland specialist species. Wetter plots showed tenfold higher abundance of obligate wetland species than those adjacent to the ditch. Moreover, facultative and obligate wetland species (e.g., sedges and rushes,

Table 3. Results of indicator species analysis for each treatment combination.

Treatment combination	Species	Indicator species value	Wetland status and habit[†]
Unfertilized/mowed/farther from ditch	*Rhynchospora inexpansa*	0.859	FACW, G
	Scleria minor	0.742	FACW, G
	Andropogon virginicus	0.707	FAC, G
	Lobelia nuttallii	0.667	FACW, F
	Solidago stricta	0.652	OBL, F
	Euthamia caroliniana	0.370	FAC, F
	Aristida virgata	0.365	FACW, G
	Eupatorium rotundifolium	0.317	FAC, F
	Rhexia mariana	0.305	FACW, F
	Pycnanthemum flexuosum	0.172	FACW, F
Unfertilized/mowed/adjacent to ditch	*Packera tomentosa*	0.586	FACU, F
	Dichanthelium scoparium	0.517	FACW, G
	Solidago pinetorum	0.500	FACU, F
	Solidago rugosa	0.339	FAC, F
Fertilized/mowed/farther from ditch	*Juncus biflorus*	0.585	FACW, G
	Eupatorium recurvans	0.344	FACW, F
	Dichanthelium dichotomum var. *dichotomum*	0.300	FAC, G
	Juncus effusus	0.285	OBL, G
	Carex glaucescens	0.254	OBL, G
	Ludwigia alternifolia	0.229	OBL, F
Fertilized/mowed/adjacent to ditch	*Rubus argutus*	0.561	FAC, S
	Rhus copallinum	0.318	UPL, S/T
	Arundinaria tecta	0.299	FACW, G
	Eupatorium semiserratum	0.238	FACW, F
Unfertilized/unmowed/farther from ditch	*Cyrilla racemiflora*	0.257	FACW, T
	Nyssa sylvatica	0.251	FAC, T
	Vaccinium corymbosum	0.250	FACW, S
Unfertilized/unmowed/adjacent to ditch	*Smilax rotundifolia*	0.343	FAC, V
	Prunus serotina	0.326	FACU, T
	Clethra alnifolia	0.299	FACW, S
Fertilized/unmowed/farther from ditch	*Chasmanthium laxum*	0.267	FACW, G
	Aronia arbutifolia	0.250	FACW, S
	Pteridium aquilinum	0.196	FACU, F
Fertilized/unmowed/adjacent to ditch	*Liquidambar styraciflua*	0.203	FAC, T

† Wetland status abbreviations are OBL, obligate wetland, almost always occurs in wetlands; FACW, facultative wetland, usually occurs in wetlands; FAC, facultative, occurs in wetlands and non-wetlands; FACU, facultative upland, usually occurs in uplands; UPL, upland, almost never occurs in wetlands. Plant habit abbreviations are G, graminoid; F, forb; S, shrub; T, tree; V, vine; P, pteridophyte.

Cyrilla racemiflora) were common indicator species of plots farther from the ditch, and an obligate upland species, *Rhus copallinum*, was an indicator for drier plots adjacent to the ditch. Other studies have found similar effects of altered hydrology on plant community diversity and composition in wetlands (Murphy et al. 2009, El Madihi 2017). For example, in a study of wetlands in a Chinese agricultural region, ditch-impacted communities showed lower diversity and greater incursion of upland species (Lu et al. 2009).

As with drainage, the negative effect of fertilization on diversity also appears to be due, in part, to the loss of wetland specialists, although the effects are evident only in mowed plots (fertilizer × mowing interaction). The mean abundance of wetland specialists in fertilized/mowed plots was less than half of that in unfertilized/mowed plots. Similar trends are seen in wetland fen habitats, where experimental nutrient addition caused generalist species to overtake habitat specialists (Pauli et al. 2002).

Table 4. Effect of factors on aboveground biomass.

Source of variation	df	X^2	P
Fertilizer	1	49.866	<0.001
Year	1	6.116	0.013
Ditch	1	28.775	<0.001
Fertilizer × Year	1	30.592	<0.001
Fertilizer × Ditch	1	0.020	0.889
Year × Ditch	1	3.496	0.062
Fertilizer × Year × Ditch	1	1.633	0.201

Note: Results of analysis of deviance.

Loss of wetland species abundance with drainage and fertilization might reflect environmental filtering (Weiher et al. 1998, Kraft et al. 2015) for species adapted to specific soil conditions. Alternatively, slow-growing plants adapted to the nutrient-poor and inundated conditions of wetlands (Aerts and Chapin 1999) might be outcompeted by more rapidly growing generalist species that thrive when plots are drained and fertilized. Consistent with this argument, plots adjacent to the ditch had greater aboveground biomass. Further, fertilization may be diminishing the inundation of undrained plots through higher production and a resulting increase in evapotranspiration (Murray et al. 2006), leading to declines in wetland plant species abundance.

Treatment effects on succession

Fertilization and ditch drainage also had similar effects on the rate of successional change. Without disturbance, the transition toward a woody community (represented primarily by PCoA axis 1; Fig. 4) was accelerated by fertilization and occurred more rapidly in drier plots. Indeed, fertilized/unmowed plots adjacent to the ditch, for which the sole current indicator species is the rapidly growing sweet gum tree, transitioned quickly at first and have changed little in composition since 2007 (Fig. 4B, triangles). In contrast, unfertilized plots that are less well drained are experiencing a slower, ongoing change in composition (Fig. 4A, circles), and current indicator species include herbaceous species (a grass and a fern).
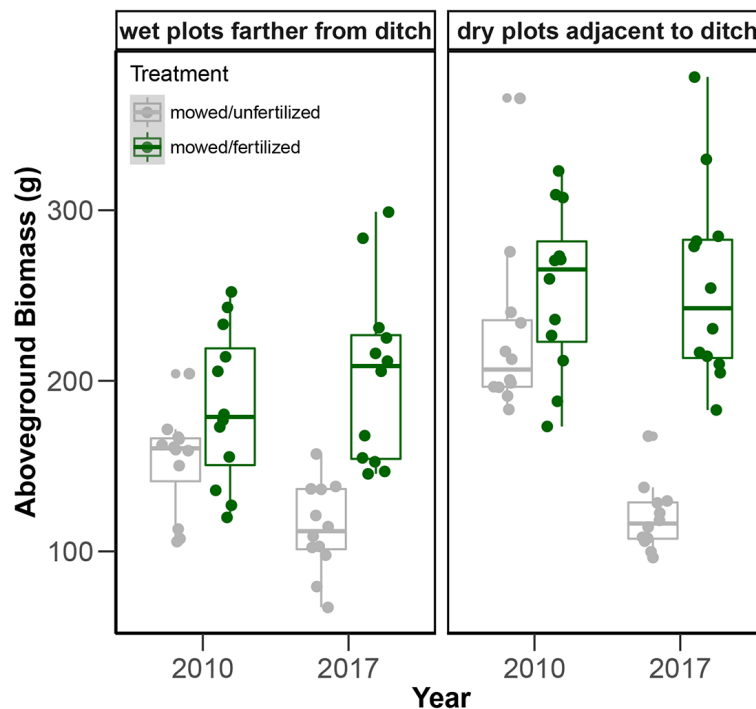

Fig. 5. Effects of fertilization and ditch proximity on aboveground biomass. Dried aboveground biomass was sampled from 0.25-m^2 quadrats in mowed and mowed/fertilized plots only. Data for individual quadrats are shown as points on box plots.

Although studies of nutrient availability and its effects on succession have had variable outcomes, plant communities in nutrient-poor habitats generally show accelerated succession when fertilized, consistent with our study (reviewed in DiTomasso and Aarssen 1989). In a classic study of old-field succession along an experimental nitrogen gradient, Tilman (1987) found that nutrient addition caused old fields to progress more rapidly to dominance by woody plants and long-lived perennials. The observed pattern suggests that soil nutrient availability, which has been shown to increase during secondary succession, is a major determinant of community dynamics (Inouye et al. 1987, Tilman 1987). Consistent with our findings, woody encroachment during a drought period was greatest in Appalachian wetland sites with the lowest water levels (Warren et al. 2007) and ditching in peat bogs has been shown to induce rapid succession to a tree-dominated community (Laine et al. 1995, Murphy et al. 2009). More generally, our results support the concept that initial abiotic conditions can influence the successional trajectories of plant communities (Douma et al. 2012).

Implications for anthropogenic impacts

The community dynamics we documented suggest that coastal plain wetland plant communities undergoing nutrient enrichment are vulnerable to loss of wetland specialists and overall diversity. Other studies have looked directly at the effects of atmospheric inputs and found congruent outcomes. For example, a study of N deposition in acid grasslands estimated that for each 2.5 kg/ha added annually, one species is lost, with species adapted to infertile conditions the most likely to be extirpated (Stevens et al. 2004). Alarmingly, total N deposition for some North Carolina coastal plain areas may be as high as >20 kg/ha annually, a value that is comparable to the fertilization rate in our experiment (National Atmospheric Deposition Program 2019).

Further, the finding of dramatically reduced diversity and loss of wetland specialists in proximity to a drainage ditch draws attention to the potential costs to natural communities of this common practice. In our experiment, the ditch effects were quite limited spatially; species diversity and wetland specialist abundance increased dramatically at only 25 m from the ditch.

However, deeper ditches are expected to impact larger areas. The results of experimental hydrology manipulations (De Steven et al. 2010, Sonnier et al. 2018) suggest that hydrologic restoration, such as filling ditches, can promote plant diversity. On the other hand, ditches themselves can serve as refuges for uncommon wetland species in human-altered landscapes (Meier et al. 2017, Rasran and Vogt 2018); thus, the conservation implications of ditch management may be complex.

Importantly, our findings suggest that fertilization and hydrological manipulation can interact to affect the trajectory and rate of succession when disturbance is suppressed. Prevention of historic wildfire regimes threatens herbaceous wetland plant communities of the coastal plain (Van Lear et al. 2005). The results of our long-term study indicate that both nutrient enrichment and drainage might accelerate changes in community composition, resulting in a more rapid transition from a diverse herbaceous wetland specialist community to one dominated by fewer generalist woody species.

CONCLUSIONS

Long-term fertilization has reduced plant species richness in a coastal plain wetland, an ecosystem for which the effects of nutrient addition are understudied. Proximity to a drainage ditch had similar effects to fertilization, and sometimes greater in magnitude. For both factors, loss of obligate wetland plant species contributed to the reduction in diversity. Complex interactions between nutrient addition, hydrology, and disturbance are evident in our results. For example, both ditch proximity and nutrient addition have acted to accelerate succession to a tree-dominated community in the absence of mowing. Our results suggest that anthropogenic nutrient additions, alteration of hydrology, and suppression of natural disturbances can have important consequences for infertile, low productivity wetland plant communities, which typically support high diversity, specialist plant communities and are therefore of priority for conservation.

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Data Availability Statement

A set of.Rmd files that include annotated code, R scripts, and data files used in this study can be found in a public GitHub repository at https://github.com/PeraltaLab/WRC_FertMowing.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3252/full