

Grazing and microhabitat interact to affect plant–plant interactions in subtropical seasonal wetlands

Elizabeth H. Boughton¹  | Pedro F. Quintana-Ascencio²  | Patrick J. Bohlen²

¹Buck Island Ranch, Archbold Biological Station, Lake Placid, FL, USA

²Department of Biology, University of Central Florida, Orlando, FL, USA

Correspondence

Elizabeth H. Boughton, Archbold Biological Station, Buck Island Ranch, 300 Buck Island Ranch Road, Lake Placid, FL 33852 USA.
Email: eboughton@archbold-station.org

Funding information

United States Department of Agriculture CSREES, Grant/Award Number: 2006-35101-17204; Environmental Protection Agency Science To Achieve Results, Grant/Award Number: F6F11250

Co-ordinating Editor: Richard Michalet

Abstract

Aims: The stress gradient hypothesis predicts that competition will be important in productive environments while facilitation will be common in environments with high stress or consumer pressure. However, abiotic stress and grazing may vary independently and even occur simultaneously. Here we examine the outcome of plant interactions in grazed wetlands where consumer pressure and abiotic stress occur concurrently. We hypothesized that cattle grazing and microhabitat would alter the outcome of plant interactions. Given that wetland edges are drier and less productive than wetland centers we expected that facilitation would be greatest in drier wetland edges due to greater abiotic stress regardless of cattle presence.

Location: Archbold Biological Station's Buck Island Ranch (BIR), south-central Florida, USA (27°09' N, 81°11' W).

Methods: We conducted an experiment for two growing seasons in ten wetlands, five exposed to cattle grazing and five fenced. Two wetland obligate plants were included (*Panicum hemitomon* and *Alternanthera philoxeroides*), and plots were assigned to three treatments (a) all neighbors removed; (b) all neighbors removed except *Juncus effusus*, a dominant, unpalatable plant; and (c) all neighbors intact (control), in both wetland centers and edges. Differences in survival, change in height and number of leaves were assessed.

Results: In ungrazed wetlands, plant survival was higher in wetland edges vs centers, while it did not differ between microhabitats in grazed wetlands. Survival in wetland edges was further increased by the presence of *Juncus effusus*. Positive interactions under grazed conditions were clear when plant height was assessed, but negative interactions affected leaf production in both ungrazed and grazed wetlands.

Conclusions: Grazing interacts with wetland microhabitat to alter plant survival. Facilitative interactions on plant height were apparent in grazed wetlands. Understanding how plant interactions change under different biotic and abiotic contexts is important for informing ecosystem restoration and management.

KEYWORDS

associational resistance, competition, facilitation, plant–animal interactions, plant–plant interactions, stress gradient hypothesis

1 | INTRODUCTION

Plant interactions range from competition to facilitation, predictably shifting to neutral or positive interactions with increasing environmental stresses or consumer pressure (Menge & Sutherland, 1976; Menge & Sutherland, 1987; Bertness & Callaway, 1994; He *et al.*, 2013). The stress gradient hypothesis (SGH) predicts that competition will be important in benign environments whereas facilitative interactions will be more common in stressful environments and those with high consumer pressure (Bertness & Callaway, 1994). In the case of productive environments with high consumer pressure (e.g., herbivory/grazing), unpalatable benefactor plants can provide facilitation via associational resistance to neighboring palatable beneficiary species (Atsatt & O'Dowd, 1976; Callaway & Aschehoug, 2000; Milchunas & Noy-Meir, 2002; Rebollo *et al.*, 2002; Oesterheld & Oyarzabal, 2004; Boughton *et al.*, 2011). In associational resistance interactions, competition and facilitation occur simultaneously and the balance is tipped one way or another depending on the level of herbivory, often showing a hump-shaped relationship where associational resistance is highest at intermediate levels of herbivory (Michalet *et al.*, 2006; Graff *et al.*, 2007; Smit *et al.*, 2007; Levenbach, 2009). Abiotic stress and herbivory typically do not occur together because the importance of consumer pressure and abiotic stress are expected to vary with productivity (consumer pressure in high-productivity environments and abiotic stress in low-productivity environments) (Grime, 1979; Filazzola *et al.*, 2018). However, an increasing number of studies document plant–plant interactions in contexts when abiotic stress and herbivory may vary independently and even occur simultaneously (Smit *et al.*, 2009; Alberti *et al.*, 2010; Howard *et al.*, 2012; He & Bertness, 2014; Filazzola *et al.*, 2018).

Herbivory and abiotic stress may occur simultaneously in ecosystems when herbivores and plants are not limited by the same abiotic stresses (Alberti *et al.*, 2010) and in systems with large herbivores (Howard *et al.*, 2012; Louthan *et al.*, 2014). For example, Alberti *et al.* (2010), showed that herbivory by crabs was greatest in more anoxic conditions and together both anoxia and herbivory affected plant distribution in a salt marsh. In a brackish marsh, it was found that combinations of herbivory by aquatic mammals and high abiotic stress (increased flooding) resulted in plant mortality (Gough & Grace, 1998). Interactions between herbivory and high abiotic stress also occur in semi-arid grasslands; for example, Veblen (2008) found that herbivory and low soil moisture interacted on a seasonal basis resulting in facilitative plant–plant interactions. Understanding how herbivory may interact with abiotic stress factors has implications for understanding how competition–facilitation processes may drive short- and long-term community change.

In freshwater seasonal wetlands, flooding and drought are fundamental factors affecting species interactions, plant growth and species distribution patterns (Voeselek *et al.*, 2004; Luo *et al.*, 2010; Merlin *et al.*, 2015). Many wetland plants are adapted to flooding and are identified as obligate wetlands plants – these plants are not stressed by flooding or anoxia but rather by drier conditions (Jung *et al.*, 2009; Luo *et al.*, 2010; Merlin *et al.*, 2015). Topographic gradients

in wetlands are thus an important factor influencing competition and facilitation between wetland species, and for obligate wetland plants, it is more likely that abiotic stress will occur at the drier wetland edges (Merlin *et al.*, 2015). Wetland edges are the transition or ecotone zone from the surrounding upland to the deeper wetland center.

Grazed wetlands are an ideal system to test how herbivory may interact with an abiotic stress gradient. Previous work showed that *Juncus effusus* var. *solutus*, an unpalatable obligate wetland plant, facilitated plant species in grazed wetlands via associational resistance (Boughton *et al.*, 2011) and maintained wetland plant diversity in grazed wetlands (Boughton *et al.*, 2011). However, the facilitative effect of *Juncus effusus* depended on competitive ability and grazing tolerance of the focal species and increased with grazing intensity (Boughton *et al.*, 2011). In addition, *Juncus effusus* has also been found to facilitate flooding-sensitive neighbors by ameliorating wet conditions via its tussock structure (Ervin, 2007). Here we examine the response of two common obligate wetland species, *Panicum hemitomon.*, a native grass, and *Alternanthera philoxeroides.*, a non-native forb, to entire plant neighborhoods and *Juncus effusus* var. *solutus* in two hydrological microhabitats (wetland center and wetland edge) in grazed wetlands and in wetlands released from grazing. These two species were previously found to benefit from associational resistance from *Juncus effusus* in grazed conditions and competed with *Juncus effusus* in ungrazed exclosures in wetland edge zones (Boughton *et al.*, 2011). A remaining question is how hydrological microhabitat may affect plant interactions with *Juncus effusus* in grazed and ungrazed contexts, with implications for understanding community change in wetland edges and centers.

We hypothesized that grazing and microhabitat would alter the outcome of plant interactions, and the relative magnitude and direction of interactions would differ among species due to their contrasting competitive abilities and palatability to cattle. Whether cattle were present or not, we expected that facilitative interactions would be more prevalent in the drier wetland edges with greater abiotic stress for wetland plants. When cattle were not present, we expected competitive interactions with neighbors to be more prevalent in wetland centers vs edge zones.

2 | METHODS

2.1 | Study site

This study took place at the Archbold Biological Station's Buck Island Ranch (BIR), located in south-central Florida, USA (27°09' N, 81°11' W), a 4252-ha commercial cattle ranch. The climate is subtropical with a mean annual temperature of 22°C (1998–2008). Mean annual precipitation is 1,218 mm (1992–2008), of which 69% falls during the wet season (June–October). Species nomenclature follows Wunderlin *et al.* (2003).

The ranch has 630 isolated, mostly small freshwater seasonal wetlands embedded throughout the property. Approximately half of the land area of BIR is occupied by intensively managed pastures (IPs)

and the other half is occupied by less intensely managed semi-natural pasture. IPs are composed primarily of Bahia grass (*Paspalum notatum*), an introduced forage grass, are usually fertilized periodically with N (~26 kg/ha), and were historically fertilized annually also with P (1960s–1986, 40 kg P₂O₅/ha). In wetlands embedded in IPs, wetland edges are dominated by *Juncus effusus*, a native tussock-forming species that cattle generally avoid, and wetland centers are dominated by emergent vegetation (e.g., *Pontederia cordata*). Wetlands in IPs are generally very similar in species composition because of nutrient addition, upland conversion, and higher cattle stocking rates (Medley *et al.*, 2015). Cattle rarely graze *Juncus effusus* and preferentially graze between *Juncus effusus* tussocks (Humphrey & Patterson, 2000; Boughton *et al.*, 2011). The presence of *Juncus effusus* depends to some degree on selective cattle grazing of surrounding species; in five-year grazing exclosures within IPs, *Juncus effusus* declined significantly while *Panicum hemitomon* and other wetland grasses became dominant (Sonnier *et al.*, 2020). The land has been used for cattle production since the 1920s. During this study (2007–2008), the average stocking rate was 0.51 animal units ha⁻¹ for the improved pastures with embedded study wetlands, but stocking rate of individual embedded wetlands is not known since data on stocking rate is collected at the pasture scale. Cattle are rotationally grazed, with cattle movement decisions based on stubble height of pasture grasses. Wetlands and surrounding pastures do not show signs of overgrazing, such as bare ground or extremely low stubble height.

2.2 | Experimental design

This experiment utilized ten wetlands, on average about 0.81 ± 0.34 ha, embedded in IPs. These wetlands are a subset

of those described in Boughton *et al.* (2011) and Boughton *et al.* (2016). Five of the wetlands were open to grazing and five were fenced to exclude grazing (hereafter, ungrazed; fencing occurred in January 2007). Fencing did not exclude other mammalian herbivores such as rabbits, deer, and feral swine, which are common throughout the study site. The study was conducted over two growing seasons (May–September) in 2007 and 2008. To characterize the environmental context of study wetlands, biomass and soil were collected in each wetland. Biomass was collected in both grazed and ungrazed wetlands in October 2007 and 2008 in five stratified random 0.25-m² circular plots in all ten wetlands. Wetlands were divided into sections: center, and four edge sections identified by cardinal directions (north, south, east, west; Figure 1). Wetland edges covered more area than wetland centers, so more biomass samples were taken in the edge zone to estimate average biomass. Biomass was clipped to the ground surface and separated by species. In March 2007, just after fencing and when all wetlands had been recently exposed to grazing, two 0–15-cm soil cores were taken near each future biomass collection location and analyzed for organic matter and soil total nitrogen (N) and total phosphorus (P). Organic matter was determined on dried, 0.5-kg subsamples by ashing for 16 hr at 450°C in a muffle furnace via the loss-on-ignition protocol. Ash was analyzed for total P (Allen *et al.*, 1974) by extracting with aqua regia (Murphy & Riley, 1962). A microplate spectrophotometer (μQuant Microplate Spectrophotometer, BioTek Instruments, Winooski, VT, USA) was used to analyze samples for total P using a modified malachite green method (D'Angelo *et al.*, 2001). Total N was analyzed at the Analytical Chemistry Laboratory at the University of Georgia, USA. The Micro-Dumas combustion technique was used, and samples were analyzed on a Carlo Erba NA 1500 CHN Analyzer (Carlo Erb, Val de Reuil, France).

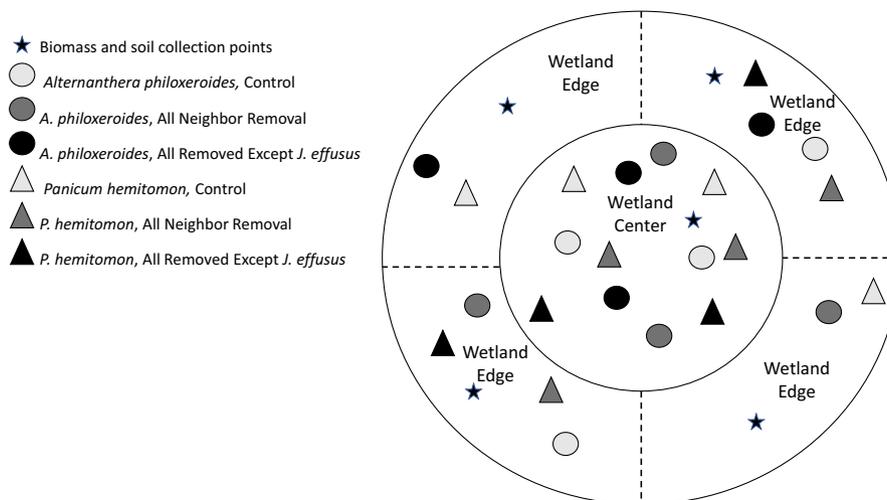


FIGURE 1 Experimental design representing one wetland in the experiment. Each year (2007 and 2008), 24 plots were established in each wetland, twelve each with *Alternanthera philoxeroides* and *Panicum hemitomon*. Each study species had two replicates of each of the neighbor manipulation treatments (1, control; 2, all neighbor removal; 3, all neighbors removed except *Juncus effusus*) at each hydrological microhabitat (edge and center). Soil sampling occurred once at the beginning of the study to characterize soil nutrients at the two microhabitats (center and edge). Biomass collection occurred once each year of the study at the end of the growing season

Within each wetland, 24 plots of 0.75 m² were randomly located in May of 2007 and May 2008, 12 plots for following target individuals of *Alternanthera philoxeroides* and 12 plots for following target individuals of *Panicum hemitomon* (Figure 1). Plots were also stratified by microhabitat (wetland edge and wetland center) to understand how plant interactions are affected at the ends of the hydrological gradient (dry edge and wet center). Wetland elevations and bathymetry were variable, but on average the elevation difference between the wetland edge and wetland center plots was 22 ± 11 cm (mean \pm SD). At different plots per microhabitat (center or edge), three clipping treatments were established in May of each year: (a) Removal – All neighbors removed; (b) Control – no removal, neighborhood intact; and (c) *Juncus* – *Juncus effusus* kept, all other neighbors removed. Removal of neighbors was conducted by clipping all biomass to the ground around the marked target plants (described below). In *Juncus* plots, all neighbors were removed by clipping everything except *Juncus effusus* around target plants. Plant removals to maintain clipping treatments occurred in May and June. All unwanted above-ground biomass was clipped to the ground level and was removed from plots. Edge and center plots that were chosen for inclusion in the study all had similar species compositions typical of wetlands in improved pastures. Wetlands in improved pastures have been found to be quite homogeneous (Boughton *et al.*, 2010; Medley *et al.*, 2015); dominant species in the study plots were *Juncus effusus*, *Alternanthera philoxeroides*, *Panicum hemitomon*, *Pontederia cordata*, and *Persicaria punctata*. All plots initially contained about 50% *Juncus effusus*, so in the *Juncus* treatment plots, approximately half of the plot area was covered by *Juncus effusus* while all other neighbor biomass was removed. This experimental design resulted in 240 plots in the experiment in each year, 2007 and 2008 (480 total) (2 grazing treatments \times 2 species \times 2 microhabitats \times 3 neighbors \times 2 years \times 10 wetlands = 480 plots) (Figure 1). In each year, different random plots were selected.

Within each treatment plot (Removal, Control, or *Juncus*), three stems of a target species (*Alternanthera philoxeroides* or *Panicum hemitomon*) were marked with wire, and height and number of leaves were recorded in May 2007 and 2008, and September for 2007, and July in 2008. For survival calculations, plots were marked as either dead or alive in September or July for 2007 and 2008, respectively. If the marked stem of all three plants could not be found or if all three marked individuals in a plot were entirely brown during a census, the plot was marked as dead. Measurements of height and number of leaves of the three marked stems were averaged for analysis, considering only the surviving tillers. Height was measured as a response because it is an indicator of a species' ability to compete for light, growth rate and as an indicator of grazing pressure (Weiher *et al.*, 1999). Number of leaves was chosen as a response because it is an indicator of a species' ability to compete for light and as an indicator of biomass (Poorter *et al.*, 2012).

2.3 | Statistical analysis

Linear mixed-effects models were used to analyze the biomass and soil nutrients of the study wetlands. Total above-ground biomass, organic matter, and soil total N and P were assessed by grazing (grazed or ungrazed) and microhabitat (center and edge) with wetland as a random effect. Grazing was not expected to significantly affect soil attributes since samples were taken just two months after grazing exclusion. Thus this test was conducted to understand if there were pre-existing soil differences in the study wetlands and if there were differences in soil attributes between center and edge hydrological locations. Wetland above-ground biomass that was collected in October was averaged for 2007 and 2008 prior to analysis and two outliers were removed to improve the model assumption of homogeneity of variance (Appendix S1); this was the only analysis for which outliers were removed.

Survival was assessed using generalized linear mixed models with a logit link, binomial error distribution, and random effects in the intercept by wetland (R package *lme4*; function "glmer"). Nine models were constructed to assess main effects and hypothesized interactions between factors. The model set included complex models (some with two interactions) and simpler nested models as well as a null model. Models tested were based on a priori hypotheses. The whole model set is presented in Appendix S2. The Akaike information criterion corrected for small sample size (AICc) was used in model selection (Bates, Mächler, Bolker, Walker R package, *bblme* 2015; function "AICcctab") to identify the most informative model (Akaike, 1973; Burnham & Anderson, 2001). The model with the lowest AICc was selected as the most likely model. For survival, we could only assess main effects and some selected interactions of four variables (species, grazing, hydrological microhabitat, and clipping treatment) because the analysis did not converge when year was included in the models.

Twenty-nine linear mixed-effects models (Pinheiro, Bates, DebRoy, Sarkar, R Core Team, *nlme* 2020, function "lme") were constructed to assess the main effects of species, year, grazing, clipping treatment, and microhabitat on the change in height and change in leaf count, with wetland as a random factor. Change in height and leaves were natural log-transformed prior to analysis to approach a normal distribution. Year effects estimated environmental variation between years. The first year of the study was a drought year with just 57% of the annual average precipitation and the second year was normal with 98% of the average precipitation. The model set included complex models (some with two or three interactions) and simpler nested models as well as a null model. Models tested were based on a priori hypotheses. The whole model sets are presented in Appendix S3. Akaike information criterion corrected for small sample size (AICc) was used in model selection (R package *bblme*; function "AICcctab") to identify the most likely model (Akaike, 1973; Burnham & Anderson, 2001). The model with the lowest AICc was selected as the most likely model. All analyses were conducted in the R statistical environment, version 4.0.2 (R Core Team, 2017).

3 | RESULTS

3.1 | Environmental context of study wetlands

Total standing above-ground biomass was clearly affected by grazing (ungrazed [mean \pm SD; thereafter except where indicated] = 777.64 ± 120.1 g/m² and grazed = 440.6 ± 166.9 g/m²; coefficient \pm SE = -362.4 ± 107.1), but we did not find evidence of clear above-ground biomass differences between wetland center and edge (edge = 634.9 ± 204.9 g/m² and center = 576.9 ± 255.4 g/m²; coefficient \pm SE = 35.3 ± 101.6 ; Figure 2a). Soil total N (edge = 512.5 ± 97.7 g/m² and center = 670.4 ± 156.3 g/m²; coefficient \pm SE = -223.3 ± 81.6), soil total P (edge = 13.5 ± 4.7 g/m² and center = 19.4 ± 6.4 g/m²; coefficient \pm SE = -7.4 ± 3.6), and organic matter (edge = 9.8 ± 1.96 g/m² and center = 19.5 ± 8.8 g/m²; coefficient \pm SE = -13.2 ± 3.5) all were greater in wetland centers vs edges (Figure 2b–d). There was no evidence of differences in soil nutrients between grazed and ungrazed wetlands. This is not surprising since soil sampling occurred just two months after cattle were excluded.

3.2 | Survival in response to grazing, microhabitat, and neighbors

The most plausible model describing survival of *Panicum hemitomon* and *Alternanthera philoxeroides* included species, an interaction between

grazing and microhabitat, and clipping treatment (Appendix S2; Figure 3; Table 1). In general, *Panicum hemitomon* had greater survival than *Alternanthera philoxeroides*. Plants had higher survival in *Juncus* treatment plots compared to Removal and Control plots. Removal plots had slightly higher survival than the controls. The interaction between grazing and microhabitat indicated higher survival in edge vs center plots in ungrazed wetlands but there was no evidence of clear difference in survival between edge and center in grazed wetlands.

3.3 | Change in height and leaves in response to grazing, microhabitat, and neighbors

The most plausible model describing change in height was an interactive model containing clip treatment, grazing, and year (model weight = 0.47, Appendix S3; Figure 4; Table 2). Clipping interacted with grazing where there was no difference among clipping treatments in ungrazed wetlands, while change in height was greater in control and *Juncus* plots compared to removal in grazed wetlands (Appendix S4). A clear interaction between year and grazing showed greater change in height in ungrazed wetlands in 2007, but there was no difference in change in heights in grazed and ungrazed wetlands in 2008 (Appendix S4; Table 2). There was no clear effect of species or microhabitat and these factors were removed from the most likely model.

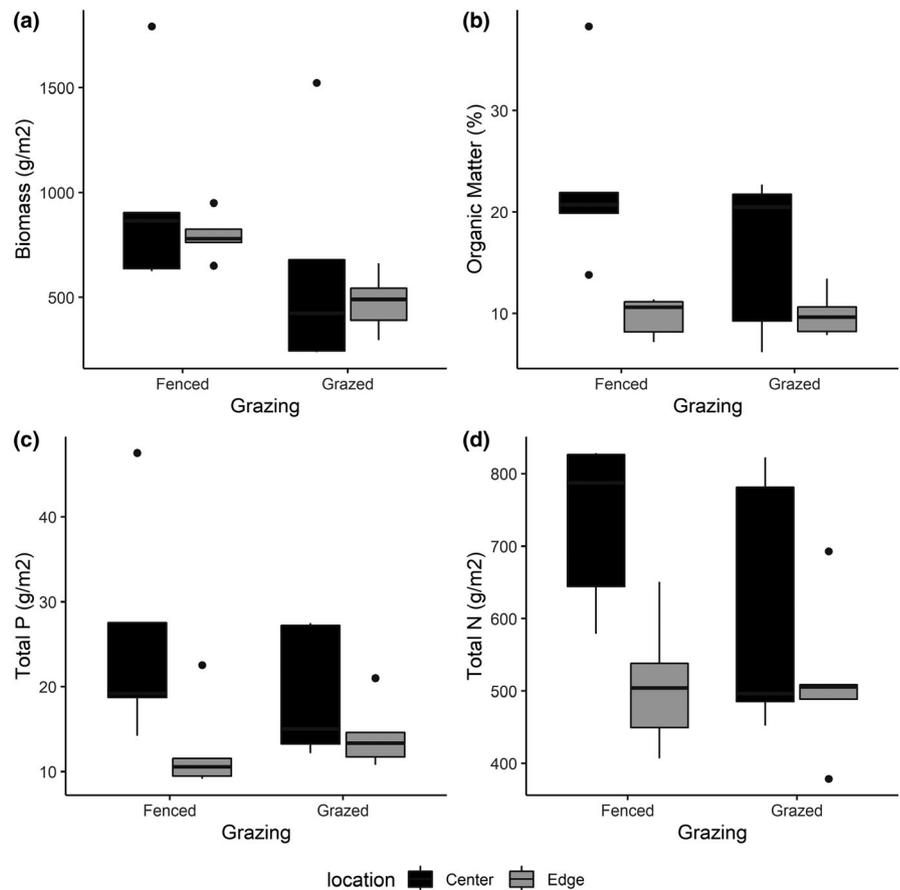


FIGURE 2 Variation in total above-ground biomass (g/m²), organic matter (%), total P (g/m²), and total N (g/m²) in grazed and ungrazed wetlands and in wetland centers and edges, where the experiment was conducted. Biomass is the average of data collected in the study wetlands in 2007 and 2008. Soil data were collected in 2007, just after fencing; thus, these data are provided for a visual representation that grazed and ungrazed wetlands were similar for the study and the main differences in soil were due to hydrologic position. Elevation difference between wetland center and edge is on average 0.22 m

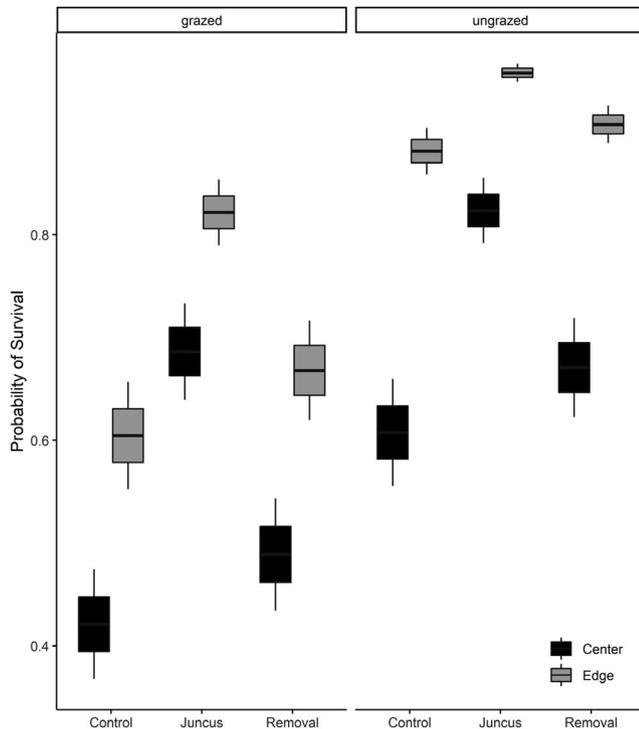


FIGURE 3 Box and whisker plot of probability of survival in grazed and ungrazed wetlands by microhabitat (edge, center) and treatment (Control, Juncus, and Removal)

TABLE 1 Results of the general linear model of survival in relation to species, clipping treatment, microhabitat, grazing

Fixed effects	Estimate	Std. error	Z value	p
Control; <i>Alternanthera</i> , grazed; 2007 (intercept)	-0.54	0.34	-1.57	0.12
Species (<i>Panicum</i>)	0.44	0.22	1.99	0.05
Grazing (ungrazed)	0.76	0.42	1.84	0.07
Microhabitat (edge)	0.75	0.28	2.65	0.008
Clipping (<i>Juncus</i>)	1.11	0.28	3.98	<0.001
Clipping (Removal)	0.28	0.26	1.08	0.28
Ungrazed: edge	0.83	0.48	1.74	0.08

Wetland ID was included as a random effect (0.479 SD). The two years of data were combined because results did not converge when year was included in the model.

The most plausible model describing change in leaves contained interactions of species, grazing, and year, and an additive effect of clipping treatment (model weight = 0.68, Appendix S3, S4; Figure 5; Table 3). Control plots had the lowest change in the number of leaves for *Alternanthera philoxeroides* for both growing seasons. A three-way interaction between species, grazing, and year indicated that *Panicum hemitomon* leaves increased more in ungrazed wetlands in the first year compared to the second year, while there was no evidence of difference in *Alternanthera philoxeroides* leaves among years or grazing treatments (Appendix S4; Figure 5; Table 3).

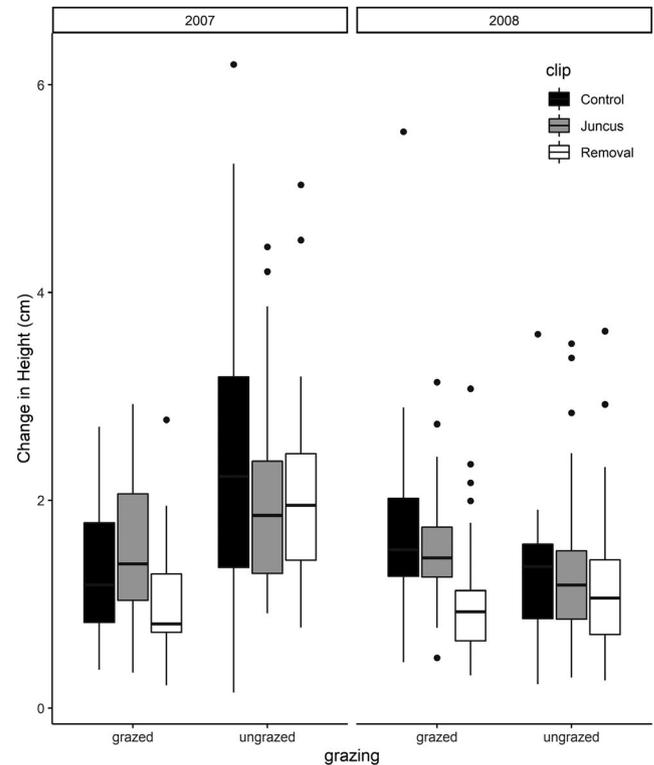


FIGURE 4 Box and whisker plot of change in plant height in the three treatments (Control, Juncus, and Removal) in grazed and ungrazed wetlands in the two years of the study

4 | DISCUSSION

4.1 | Did grazing and microhabitat interact to affect plant-plant interactions?

It was expected that wetland edge and center microhabitats would have different abiotic stress levels for obligate wetland plants, with increased abiotic stress (dryness) in wetland edges. Further, we expected that microhabitat would interact with grazing and clipping treatment to show a prevalence of facilitative interactions in grazed wetland edges. For plant survival, the most plausible model contained an interaction of grazing and microhabitat that, in part, supports this hypothesis. However, clipping treatment did not interact with microhabitat or grazing, but was a clear main effect, showing higher survival with Juncus (i.e., facilitation) regardless of microhabitat or grazing.

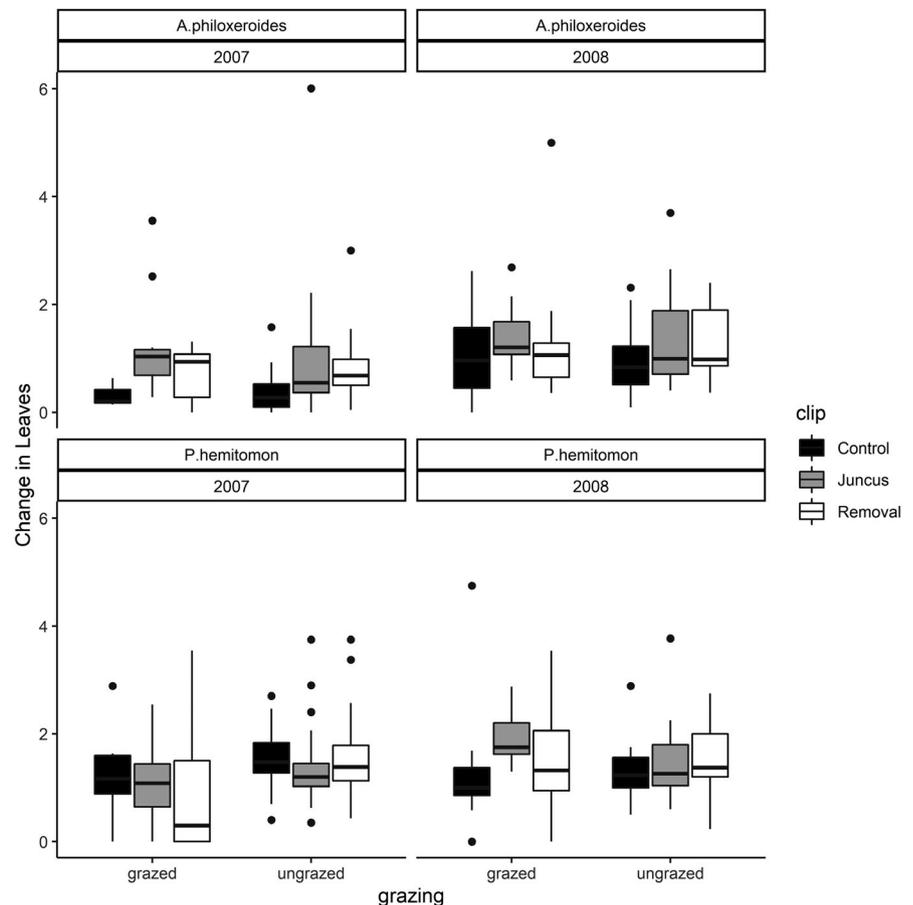
In the absence of grazing, both species had higher survival in wetland edges compared to wetland centers. In contrast, in grazed wetlands, there was no evidence of a difference in survival between wetland edges and centers. Soil nutrient data showed that microhabitat in seasonal wetlands covaried with several plant resources. Soil nutrients (N and P) and organic matter were greatest in wetland centers where wetland hydroperiod was longest. Additionally, ungrazed wetlands have almost twice the standing biomass compared to grazed wetlands (Sonnier *et al.*, 2020). Taken together, ungrazed wetland centers, with higher nutrients and presumably productivity, negatively impacted plant survival, possibly due to increased light

TABLE 2 Results of the linear mixed effects model for change in height selected as the most plausible model in the AICc model selection (see Appendix S3)

Fixed effects	Estimate	Std. error	df	t value	p
Control; grazed; 2007 (intercept)	0.15	0.16	322	0.91	0.36
Clip (<i>Juncus</i>)	0.13	0.19	322	0.69	0.49
Clip (Removal)	-0.25	0.22	322	-1.09	0.27
Grazing (ungrazed)	0.54	0.19	8	2.75	0.03
Year (2008)	0.29	0.18	322	1.63	0.10
<i>Juncus</i> : ungrazed	-0.18	0.23	322	-0.76	0.45
Removal: ungrazed	-0.22	0.26	322	0.82	0.41
<i>Juncus</i> : 2008	-0.18	0.23	322	-0.78	0.44
Removal: 2008	-0.32	0.26	322	-1.23	0.22
Ungrazed: 2008	-0.85	0.23	322	-3.71	<0.001
<i>Juncus</i> : ungrazed: 2008	0.19	0.29	322	0.66	0.51
Removal: ungrazed: 2008	0.18	0.33	322	0.56	0.57

Wetland ID was included as a random effect = 0.09 SD, residual = 0.53.

FIGURE 5 Box and whisker plot of change in leaves of the two study species in the three treatments (Control, *Juncus*, and Removal) in grazed and ungrazed wetlands in the two years of the study



competition, while lower moisture and nutrients in wetland edges may have decreased competitive interactions resulting in greater survival in ungrazed wetland edges. Herbaceous wetlands are known to be highly productive ecosystems where competition for light can drive community composition (Grime, 1979; Bernard *et al.*, 1988). Additionally, Perry & Galatowitsch, 2004 found that light limitation

can alter plant-plant competitive interactions in sedge meadow vegetation. In this study, higher survival in ungrazed wetland edges suggests that abiotic stress due to the moisture gradient was less important than increased competition for light in wetland centers. Mechanistically, our data suggest that in ungrazed wetlands during the wet season, competition is lower in wetland edges resulting in

Fixed effects	Estimate	Std. error	df	t value	p
Control; <i>Alternanthera</i> , grazed; 2007 (intercept)	0.48	0.08	324	5.66	0.00
Species (<i>Panicum</i>)	0.07	0.10	324	0.75	0.45
Grazing (ungrazed)	-0.06	0.09	8	-0.66	0.53
Year (2008)	0.19	0.09	324	2.13	0.03
Clip (<i>Juncus</i>)	0.15	0.04	324	3.42	<0.001
Clip (Removal)	0.09	0.05	324	1.95	0.05
<i>Panicum</i> : ungrazed	0.32	0.12	324	2.60	0.01
<i>Panicum</i> : 2008	0.05	0.12	324	0.41	0.69
Ungrazed: 2008	0.04	0.11	324	0.37	0.71
<i>Panicum</i> : ungrazed: 2008	-0.31	0.15	324	-2.03	0.04

TABLE 3 Results of the linear mixed effects model for change in number of leaves selected as the most plausible model in the AICc model selection (See Appendix S3)

Wetland ID was included as a random effect = 0.03 SD, residual = 0.33. Significance level is $p=0.05$.

increased plant survival compared to wetland centers. However, further work is needed to confirm if light limitation differs in ungrazed wetland edges vs centers. Other studies have also found that increased abiotic stress can reduce the magnitude of plant-plant interactions, both facilitative and competitive. For example, Soliveres *et al.* (2010) found that the magnitude of competition was reduced under low rainfall on drier, south-facing slopes in semi-arid ecosystems and Filazzola *et al.* (2018) found that the magnitude of facilitation by shrubs was reduced in an extreme drought year compared to years of normal precipitation.

On the other hand, in grazed wetlands, grazing may reduce competition for light between plants in wetland centers and allow similar survival of species at either end of the hydrological gradient. Many studies have shown that grazing reduces light competition among plants with resulting impacts on both populations and communities (van der Wal *et al.*, 2000; Koerner *et al.*, 2018). van der Wal *et al.*, 2000 found that herbivore exclusion increased the effects of plant competition, lowering plant performance in highly productive and competitive salt marshes. In addition to reducing competitive ability of neighbors, grazing also reduces vegetation height leading to increased light availability (McNaughton, 1992). Koerner *et al.* (2018) showed that grazing maintained species diversity in grasslands exposed to nutrient addition through the reduction of dominant species and an altered competitive environment.

Survival in wetland edges in both ungrazed and grazed wetlands was increased by the presence of *Juncus effusus*, indicating facilitative interactions. Positive impacts of *Juncus effusus* on survival in ungrazed conditions were unexpected since previous studies showed *Juncus effusus* facilitated species by associational resistance under grazed conditions (Boughton *et al.*, 2011; Boughton *et al.*, 2011). *Juncus effusus* may benefit species through other mechanisms such as reduction of microclimatic stress (Filazzola *et al.*, 2018) but further work is necessary to understand the mechanisms driving plant-plant interactions with *Juncus effusus*.

Interestingly, there was no clear impact of the interaction of microhabitat and grazing on plant interactions when plant growth metrics were considered. This lack of evidence of an impact of the microhabitat on plant interactions in seasonal wetlands may be due to the short length of this stress gradient. Other studies have emphasized the need for studying a sufficiently long stress gradient to detect facilitation (Le Bagousse-Pinguet *et al.*, 2012). Another plausible explanation may be related to the dynamic nature of seasonal wetlands for which these species are adapted. Seasonal wetlands in the southeastern Coastal Plain of the U.S. are shallow basins with hydrology primarily driven by rainfall and shallow subsurface water flow (Lide *et al.*, 1995). These dynamic ecosystems typically experience both flooded and dry conditions each year. Therefore, plant and animal species found within these wetlands are adapted to the cycles of wetting and drying (Kirkman & Sharitz, 1994). The species included in this study were found across the wetland hydrology gradient; for example, *Panicum hemitomon* occurs in water depths ranging from 0 cm to 55 cm with highest cover values between 40 cm and 55 cm, and *Alternanthera philoxeroides* occurs in depths ranging from 0 cm to 58 cm, with highest cover values in ~30 cm to 40 cm of water (Boughton, unpublished data). Therefore, both species are tolerant of a wide range of hydrological conditions and may not experience intense abiotic stress in these seasonal wetlands, even though they are flooding-tolerant obligate wetland plants. It is important to note that this study was conducted during the wet season in Florida and different dynamics and levels of abiotic stress may occur in the dry season (Lovell & Menges, 2013). It is possible that during the dry season, abiotic stress would be even more intense and seasonal changes could impact the relative importance of facilitation and competition in wetland plant communities, with facilitation likely more prevalent in the dry season and competition important for structuring wet-season plant communities. Lovell and Menges (2013) found that the availability of soil water and not competitive interactions dictated growth and survival in the dry season in seasonal wetlands. That study also included *Panicum hemitomon* which exhibited decreased



growth rate and increased resprouting, and increased mortality of resprouted ramets in the driest month. In contrast, the results of our study, conducted in the wet season, showed that competition was important for structuring plant communities mainly by impacting plant survival in wetland centers. Taken together, these two studies point to the need for assessing the impact of plant–plant interactions throughout annual hydrological cycles.

4.2 | Impact of grazing on plant interactions

Our results showed that the outcome of plant–plant interactions under grazed and ungrazed conditions depended on the growth parameter assessed. Positive outcomes among interactive plants were more apparent in measurements of plant height vs leaf production. There was greater change in height in *Juncus* and Control plots compared to Removal plots in grazed wetlands, but no major differences among treatments in ungrazed wetlands. This result suggests that protection from grazing by surrounding plant neighbors is important to determine plant height and aligns with numerous previous studies that have documented the prevalence of facilitation under grazed conditions (Boughton *et al.*, 2011; Graff & Aguiar, 2011). Conversely, leaf production was greater in *Juncus* and Removal treatments vs Controls in both grazed and ungrazed wetlands, suggesting negative outcomes with plant–plant interactions for leaf production because plants in plots with less surrounding neighbors had greater increase in leaves.

Different outcomes of plant–plant interactions for different demographic parameters and life stages have been documented in other studies. For example, Soliveres *et al.* (2010) found that ontogenetically driven facilitation/competition shifts in long-lived perennial species are important. They found that facilitation was important in early growth stages such as germination and seedling growth while competition was more important for older shrubs. Other studies show that different processes impact leaf production, flower production, and stalk growth (Klanderud & Totland, 2005). Klanderud & Totland (2005) found that flower stems and leaf stalks became shorter while leaf number increased after removal of neighbor vegetation. The opposing responses of stalks and leaves suggest different resource allocation, after vegetation removal, with leaf production impacted by competitive interactions and stalks affected by facilitative interactions of neighbor protection (Klanderud & Totland, 2005).

5 | CONCLUSION

Current models of plant–plant interactions emphasize the impact of abiotic stress or consumer pressure on plant interactions independently. However, understanding how plant interactions change in response to multiple co-occurring factors such as abiotic stress, consumer pressure, and disturbance requires more investigation and is important for informing restoration, land management and

predicting plant communities change over time (Howard *et al.*, 2012; Bagousse-Pinguet *et al.*, 2014; Filazzola *et al.*, 2018).

Results of our study can be useful for predicting plant compositional changes if cattle grazing is removed from wetlands. About 15% of the region where this study took place is comprised of isolated seasonal wetlands, many located on private grazing lands. These grazing lands overlap some of Florida's most important conservation lands and water resources; thus, conservation and wetland restoration on ranchland is extremely important. State agencies are interested in managing and restoring isolated wetlands to improve downstream water quality and supply and to enhance wildlife habitat. Federal conservation programs, such as the United States Department of Agriculture's (USDA) Wetland Reserve Program (WRP), provide economic opportunities for ranchers to protect important wetland resources but may restrict grazing on enrolled wetlands. Florida is one of the few states that continues to allow grazing in WRP lands for vegetation management (Sonnier *et al.*, 2018). Our study shows that survival was greatest in ungrazed wetlands and that the species examined are likely to remain abundant in ungrazed wetlands at least in the short term. Maintaining *Panicum hemitomon* populations is a high priority restoration goal; however, *Alternanthera philoxeroides* is a Category II invasive plant (FLEPPC) and not desirable. In ungrazed wetlands, competition is more intense in wetland centers and negatively impacted plant survival, suggesting that *Alternanthera philoxeroides* and *Panicum hemitomon* may change their distribution in wetlands to be more abundant in wetland edges when grazing is removed or limited. In contrast, plant survival was similar in wetland edges and centers in grazed wetlands, suggesting these two common species would remain equally abundant across the hydrological gradient in grazed wetlands. Long-term data on plant species composition in wetlands released from grazing are needed to understand how wetland structure and function change when grazing is removed or limited, to inform wetland restoration and management.

ACKNOWLEDGEMENTS

United States Department of Agriculture CSREES (2006-35101-17204) and an Environmental Protection Agency STAR graduate fellowship (F6F11250) to EHB supported this work. Thanks to Christen Steele, Olivia Tabares and Aimee Fraulo for field work assistance and to John Garrett and Steffan Pierre for data preparation. Thanks to three anonymous reviewers for valuable comments that improved the manuscript. This research was a contribution from the Long-Term Agroecosystem Research (LTAR) network. LTAR is supported by the United States Department of Agriculture.

AUTHOR CONTRIBUTIONS

EHB, PFQA, and PJB conceived and designed the experiment. EHB conducted fieldwork. PFQA, and EHB analyzed the data. EHB wrote the manuscript. PFQA and PJB provided editorial advice.

DATA AVAILABILITY STATEMENT

Boughton, E.H. 2020. Grazing and microhabitat interact to affect plant–plant interactions in subtropical seasonal wetlands, 2007-2008

ver 1. Environmental Data Initiative. <https://doi.org/10.6073/pasta/598b079fb4359708af52969e8cf62fa1> (Accessed 2020-10-02). All R code is available upon request.

ORCID

Elizabeth H. Boughton  <https://orcid.org/0000-0003-0932-280X>

Pedro F. Quintana-Ascencio  <https://orcid.org/0000-0001-7587-8166>

REFERENCES

- Akaike, H. (1973) Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, 60, 255–265.
- Alberti, J., Casariego, A.M., Daleo, P., Fanjul, E., Silliman, B., Bertness, M. *et al* (2010) Abiotic stress mediates top-down and bottom-up control in a Southwestern Atlantic salt marsh. *Oecologia*, 163, 181–191. <https://doi.org/10.1007/s00442-009-1504-9>
- Allen, S.E., Grimshaw, H.M., Parkinson, J.A. & Quarmby, C. (1974). *Chemical Analysis of Ecological Materials*. Blackwell Scientific Publications.
- Atsatt, P.R. & O'Dowd, D.J. (1976) Plant defense guilds. *Science*, 193, 24–29.
- Bagousse-Pinguet, Y.L., Maalouf, J.-P., Touzard, B. & Michalet, R. (2014) Importance, but not intensity of plant interactions relates to species diversity under the interplay of stress and disturbance. *Oikos*, 123, 777–785. <https://doi.org/10.1111/oik.00961>
- Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67(1), 1–48.
- Bernard, J.M., Solander, D. & Květ, J. (1988) Production and nutrient dynamics in *Carex* wetlands. *Aquatic Botany*, 30, 125–147. [https://doi.org/10.1016/0304-3770\(88\)90011-3](https://doi.org/10.1016/0304-3770(88)90011-3)
- Bertness, M.D. & Callaway, R. (1994) Positive interactions in communities. *Trends in ecology & evolution*, 9, 191–193. [https://doi.org/10.1016/0169-5347\(94\)90088-4](https://doi.org/10.1016/0169-5347(94)90088-4)
- Boughton, E.H., Quintana-Ascencio, P.F. & Bohlen, P.J. (2011) Refuge effects of *Juncus effusus* in grazed, subtropical wetland plant communities. *Plant Ecology*, 212, 451–460. <https://doi.org/10.1007/s11258-010-9836-4>
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., Fauth, J.E. & Jenkins, D.G. (2016) Interactive effects of pasture management intensity, release from grazing and prescribed fire on forty subtropical wetland plant assemblages (T. Pärt, Ed.). *Journal of Applied Ecology*, 53, 159–170. <https://doi.org/10.1111/1365-2664.12536>
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J., Jenkins, D.G. & Pickert, R. (2010) Land-use and isolation interact to affect wetland plant assemblages. *Ecography*, 33, 461–470. <https://doi.org/10.1111/j.1600-0587.2009.06010.x>
- Boughton, E.H., Quintana-Ascencio, P.F., Bohlen, P.J. & Nickerson, D. (2011) Differential facilitative and competitive effects of a dominant macrophyte in grazed subtropical wetlands: Plant interactions in grazed subtropical wetlands. *Journal of Ecology*, 99, 1263–1271. <https://doi.org/10.1111/j.1365-2745.2011.01850.x>
- Boughton, E.H., Quintana-Ascencio, P.F., Nickerson, D. & Bohlen, P.J. (2011) Management intensity affects the relationship between non-native and native species in subtropical wetlands: Management intensity affects non-native and native relationships. *Applied Vegetation Science*, 14, 210–220. <https://doi.org/10.1111/j.1654-109X.2010.01116.x>
- Burnham, K.P. & Anderson, D.R. (2001) Kullback-Leibler information as a basis for strong inference in ecological studies. *Wildlife Research*, 28, 111–119. <https://doi.org/10.1071/WR99107>
- Callaway, R.M. & Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science*, 290, 521–523. <https://doi.org/10.1126/science.290.5491.521>
- D'Angelo, E., Crutchfield, J. & Vandivere, M. (2001) Rapid, sensitive, microscale determination of phosphate in water and soil. *Journal of Environmental Quality*, 30, 2206–2209. <https://doi.org/10.2134/jeq2001.2206>
- Ervin, G.N. (2007) An experimental study on the facilitative effects of tussock structure among wetland plants. *Wetlands*, 27, 620–630. [https://doi.org/10.1672/0277-5212\(2007\)27\[620:AESOTF\]2.0.CO;2](https://doi.org/10.1672/0277-5212(2007)27[620:AESOTF]2.0.CO;2)
- Filazzola, A., Liczner, A.R., Westphal, M. & Lortie, C.J. (2018) The effect of consumer pressure and abiotic stress on positive plant interactions are mediated by extreme climatic events. *New Phytologist*, 217, 140–150. <https://doi.org/10.1111/nph.14778>
- Gough, L. & Grace, J.B. (1998) Effects of flooding, salinity and herbivory on coastal plant communities, Louisiana, United States. *Oecologia*, 117, 527–535. <https://doi.org/10.1007/s004420050689>
- Graff, P. & Aguiar, M.R. (2011) Testing the role of biotic stress in the stress gradient hypothesis. Processes and patterns in arid rangelands. *Oikos*, 120, 1023–1030. <https://doi.org/10.1111/j.1600-0706.2010.19059.x>
- Graff, P., Aguiar, M.R. & Chaneton, E.J. (2007) Shifts in positive and negative plant interactions along a grazing intensity gradient. *Ecology*, 88, 188–199. [https://doi.org/10.1890/0012-9658\(2007\)88\[188:SIPANP\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[188:SIPANP]2.0.CO;2)
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. Plant strategies and vegetation processes.
- He, Q. & Bertness, M.D. (2014) Extreme stresses, niches, and positive species interactions along stress gradients. *Ecology*, 95, 1437–1443. <https://doi.org/10.1890/13-2226.1>
- He, Q., Bertness, M.D. & Altieri, A.H. (2013) Global shifts towards positive species interactions with increasing environmental stress. *Ecology letters*, 16, 695–706. <https://doi.org/10.1111/ele.12080>
- Howard, K.S., Eldridge, D.J. & Soliveres, S. (2012) Positive effects of shrubs on plant species diversity do not change along a gradient in grazing pressure in an arid shrubland. *Basic and Applied Ecology*, 13, 159–168. <https://doi.org/10.1016/j.baae.2012.02.008>
- Humphrey, J.W. & Patterson, G.S. (2000) Effects of late summer cattle grazing on the diversity of riparian pasture vegetation in an upland conifer forest. *Journal of Applied Ecology*, 37, 986–996. <https://doi.org/10.1046/j.1365-2664.2000.00550.x>
- Jung, V., Mony, C., Hoffmann, L. & Muller, S. (2009) Impact of competition on plant performances along a flooding gradient: a multi-species experiment. *Journal of Vegetation Science*, 20, 433–441. <https://doi.org/10.1111/j.1654-1103.2009.05786.x>
- Kirkman, L.K. & Sharitz, R.R. (1994) Vegetation disturbance and maintenance of diversity in intermittently flooded Carolina Bays in South Carolina. *Ecological Applications*, 4, 177–188. <https://doi.org/10.2307/1942127>
- Klanderud, K. & Totland, Ø. (2005) The relative importance of neighbours and abiotic environmental conditions for population dynamic parameters of two alpine plant species. *Journal of Ecology*, 93, 493–501.
- Koerner, S.E., Smith, M.D., Burkepile, D.E., Hanan, N.P., Avolio, M.L., Collins, S.L. *et al* (2018) Change in dominance determines herbivore effects on plant biodiversity. *Nature Ecology & Evolution*, 2, 1925–1932. <https://doi.org/10.1038/s41559-018-0696-y>
- Le Bagousse-Pinguet, Y., Gross, E.M. & Straile, D. (2012) Release from competition and protection determine the outcome of plant interactions along a grazing gradient. *Oikos*, 121, 95–101. <https://doi.org/10.1111/j.1600-0706.2011.19778.x>
- Levenbach, S. (2009) Grazing intensity influences the strength of an associational refuge on temperate reefs. *Oecologia*, 159, 181–190. <https://doi.org/10.1007/s00442-008-1186-8>
- Lide, R.F., Meentemeyer, V.G., Pinder, J.E. & Beatty, L.M. (1995) Hydrology of a carolina bay located on the upper coastal plain of western South Carolina. *Wetlands*, 15, 47–57. <https://doi.org/10.1007/BF03160679>

- Louthan, A.M., Doak, D.F., Goheen, J.R., Palmer, T.M. & Pringle, R.M. (2014) Mechanisms of plant–plant interactions: concealment from herbivores is more important than abiotic-stress mediation in an African savannah. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20132647. <https://doi.org/10.1098/rspb.2013.2647>
- Lovell, J.T. & Menges, E. (2013) Dominant species responses to drought in seasonal wetlands: evidence from reciprocal transplants across a moisture gradient. *The Journal of the Torrey Botanical Society*, 140, 157–169. <https://doi.org/10.3159/TORREY-D-12-00055.1>
- Luo, W., Xie, Y., Chen, X., Li, F. & Qin, X. (2010) Competition and facilitation in three marsh plants in response to a water-level gradient. *Wetlands*, 30, 525–530. <https://doi.org/10.1007/s13157-010-0064-4>
- McNaughton, S.J. (1992) Laboratory-simulated grazing: interactive effects of defoliation and canopy closure on Serengeti grasses. *Ecology*, 73, 170–182. <https://doi.org/10.2307/1938729>
- Medley, K.A., Boughton, E.H., Jenkins, D.G., Fauth, J.E., Bohlen, P.J. & Quintana-Ascencio, P.F. (2015) Intense ranchland management tips the balance of regional and local factors affecting wetland community structure. *Agriculture, Ecosystems & Environment*, 212, 207–244. <https://doi.org/10.1016/j.agee.2015.06.024>
- Menge, B.A. & Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist*, 130, 730–757. <https://doi.org/10.1086/284741>
- Menge, B.A. & Sutherland, J.P. (1976) Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *The American Naturalist*, 110, 351–369. <https://doi.org/10.1086/283073>
- Merlin, A., Bonis, A., Damgaard, C.F. & Mesléard, F. (2015) Competition is a strong driving factor in wetlands, peaking during drying out periods. *PLoS One*, 10, e0130152. <https://doi.org/10.1371/journal.pone.0130152>
- Michalet, R., Brooker, R.W., Cavieres, L.A., Kikvidze, Z., Lortie, C.J., Pugnaire, F.I. et al (2006) Do biotic interactions shape both sides of the humped-back model of species richness in plant communities? *Ecology Letters*, 9, 767–773. <https://doi.org/10.1111/j.1461-0248.2006.00935.x>
- Milchunas, D.G. & Noy-Meir, I. (2002) Grazing refuges, external avoidance of herbivory and plant diversity. *Oikos*, 99, 113–130. <https://doi.org/10.1034/j.1600-0706.2002.990112.x>
- Murphy, J. & Riley, J.P. (1962) A modified single solution method for the determination of phosphate in natural waters. *Analytica Chimica Acta*, 27, 31–36. [https://doi.org/10.1016/S0003-2670\(00\)88444-5](https://doi.org/10.1016/S0003-2670(00)88444-5)
- Oosterheld, M. & Oyarzábal, M. (2004) Grass-to-grass protection from grazing in a semi-arid steppe. Facilitation, competition, and mass effect. *Oikos*, 107, 576–582. <https://doi.org/10.1111/j.0030-1299.2004.13442.x>
- Perry, L.G. & Galatowitsch, S.M. (2004) The influence of light availability on competition between *Phalaris arundinacea* and a native wetland sedge. *Plant Ecology*, 170, 73–81. <https://doi.org/10.1023/B:VEGE.0000019019.78909.f0>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team (2020). nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-149, <https://CRAN.R-project.org/package=nlme>
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P. & Mommer, L. (2012) Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytologist*, 193, 30–50. <https://doi.org/10.1111/j.1469-8137.2011.03952.x>
- R Core Team (2017) *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Rebollo, S., Milchunas, D.G., Noy-Meir, I. & Chapman, P.L. (2002) The role of a spiny plant refuge in structuring grazed short-grass steppe plant communities. *Oikos*, 98, 53–64. <https://doi.org/10.1034/j.1600-0706.2002.980106.x>
- Smit, C., Rietkerk, M. & Wassen, M.J. (2009) Inclusion of biotic stress (consumer pressure) alters predictions from the stress gradient hypothesis. *Journal of Ecology*, 97, 1215–1219. <https://doi.org/10.1111/j.1365-2745.2009.01555.x>
- Smit, C., Vandenbergh, C., Den Ouden, J. & Müller-Schärer, H. (2007) Nurse plants, tree saplings and grazing pressure: changes in facilitation along a biotic environmental gradient. *Oecologia*, 152, 265–273. <https://doi.org/10.1007/s00442-006-0650-6>
- Soliveres, S., DeSoto, L., Maestre, F.T. & Olano, J.M. (2010) Spatio-temporal heterogeneity in abiotic factors modulate multiple ontogenetic shifts between competition and facilitation. *Perspectives in Plant Ecology, Evolution and Systematics*, 12, 227–234. <https://doi.org/10.1016/j.ppees.2010.02.003>
- Sonnier, G., Bohlen, P.J., Swain, H.M., Orzell, S.L., Bridges, E.L. & Boughton, E.H. (2018) Assessing the success of hydrological restoration in two conservation easements within Central Florida ranchland. *PLoS One*, 13, e0199333. <https://doi.org/10.1371/journal.pone.0199333>
- Sonnier, G., Quintana-Ascencio, P.F., Fauth, J.E., Jenkins, D.G., Bohlen, P.J. & Boughton, E.H. (2020) Pasture management, grazing, and fire interact to determine wetland provisioning in a subtropical agroecosystem. *Ecosphere*, 11, e03209. <https://doi.org/10.1002/ecs2.3209>
- van der Wal, R.V.D., Egas, M., Veen, A.V.D. & Bakker, J. (2000) Effects of resource competition and herbivory on plant performance along a natural productivity gradient. *Journal of Ecology*, 88, 317–330. <https://doi.org/10.1046/j.1365-2745.2000.00450.x>
- Veblen, K.E. (2008) Season- and herbivore-dependent competition and facilitation in a semiarid savanna. *Ecology*, 89, 1532–1540. <https://doi.org/10.1890/07-0973.1>
- Voesenek, L., Rijnders, J., Peeters, A.J.M., Van de Steeg, H.M. & De Kroon, H. (2004) Plant hormones regulate fast shoot elongation under water: from genes to communities. *Ecology*, 85, 16–27. <https://doi.org/10.1890/02-740>
- Weiher, E., van der Werf, A., Thompson, K., Roderick, M., Garnier, E. & Eriksson, O. (1999) Challenging Theophrastus: A common core list of plant traits for functional ecology. *Journal of Vegetation Science*, 10, 609–620. <https://doi.org/10.2307/3237076>
- Wunderlin, R.P. & Hansen, B.F. (2003). *Guide to the Vascular Plants of Florida*. University Press of Florida.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1 Rationale for excluding two outliers for above-ground biomass

Appendix S2 Model set for survival

Appendix S3 Model set for height and leaves

Appendix S4 ANOVA tables for height and leaves analysis

How to cite this article: Boughton EH, Quintana-Ascencio PF, Bohlen PJ. Grazing and microhabitat interact to affect plant–plant interactions in subtropical seasonal wetlands. *J Veg Sci.* 2020;00:1–11. <https://doi.org/10.1111/jvs.12962>