

Refuge effects of *Juncus effusus* in grazed, subtropical wetland plant communities

Elizabeth H. Boughton ·
Pedro F. Quintana-Ascencio ·
Patrick J. Bohlen

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Abstract Unpalatable plant species often act as biotic refuges by protecting neighboring plants from herbivores. This positive interaction can increase functional diversity in grazed ecosystems by protecting species sensitive to grazing. While many studies investigate pair-wise interactions between benefactors and beneficiaries, few show that these interactions result in community composition effects. We studied the effect of an unpalatable plant, *Juncus effusus*, on wetland plant communities in grazed and ungrazed plots. We tested the following predictions: (1) *Juncus* would increase plant functional diversity in grazed wetlands; (2) *Juncus* would have significant effects on community composition; and (3) the effects of *Juncus* on other species would change across the grazing gradient. We found that *Juncus* preserved functional diversity in grazed wetland communities by protecting species that decrease with grazing pressure. In multivariate analyses, grazing was the strongest driver of species composition but we found significant effects of *Juncus* on both vegetation change and species composition in grazed plots. Interactions with *Juncus* were

facilitative in grazed plots and competitive in ungrazed plots, but did not vary along the grazing gradient (0.15–1.7 cows/ha). These results indicate that *Juncus* has significant community composition effects in grazed wetland plant communities. Understanding the effects of plant interactions such as these at the community level is essential to applying plant interactions to restoration or management.

Keywords Facilitation · Herbivory · Plant–plant interactions · Stress gradients

Introduction

Unpalatable plant species often act as biotic refuges by protecting neighboring plants from herbivores (Atsatt and O’Dowd 1976; Callaway et al. 2000; Milchunas and Noy-Meir 2002; Rebollo et al. 2002; Oesterheld and Oyarzabal 2004). As biotic refuges, unpalatable plants may have important implications for diversity, conservation, and management in grazed ecosystems (Callaway et al. 2005) and may provide safe sites for species that would have been eradicated by grazing. Thus, unpalatable plants can promote stability in habitats with high consumer pressure (Callaway et al. 2000, 2005; Rebollo et al. 2002, 2005).

Often, species that are protected by unpalatable plants are palatable species that are preferred by grazers and are sensitive to grazing pressure

E. H. Boughton (✉) · P. F. Quintana-Ascencio
Department of Biology and Graduate Program
in Conservation Biology, University of Central Florida,
Orlando, FL 32816, USA
e-mail: eboughton@archbold-station.org

P. J. Bohlen
MacArthur Agro-Ecology Research Center, 300 Buck
Island Ranch Road, Lake Placid, FL 33852, USA

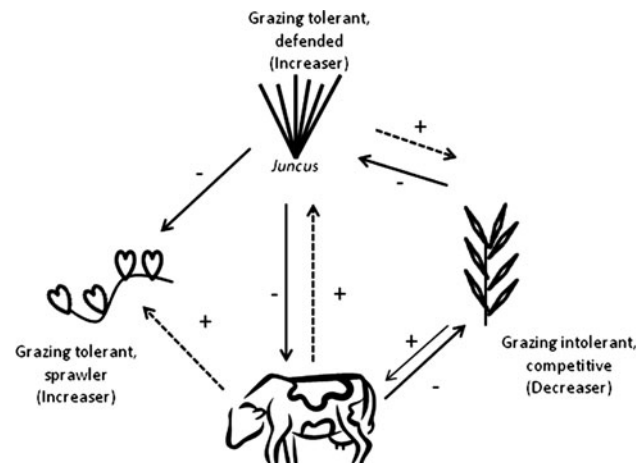


Fig. 1 Interaction web between an herbivore, *Juncus*, and increaser and decreaser species. Herbivores indirectly (*dashed lines*) benefit both increaser, grazing tolerant defended species (such as *Juncus*) and short-statured sprawling species by

reducing their competitors (*decreasers*). *Juncus* indirectly positively affects grazing-intolerant competitive species by protection from herbivory which results in a direct (*solid lines*) negative effect of *Juncus* on cattle

(Callaway et al. 2005; Baraza et al. 2006). Species have been divided into groups based on the way they respond to grazing (Olf and Ritchie 1998; McIntyre et al. 2003). Increasers are species that increase cover with grazing pressure and decreasers are species that decrease cover with grazing pressure (McIntyre et al. 2003). These two response groups relate to the adaptive strategies proposed by Grime (1977). In grazed ecosystems, biotic refuges are stress-tolerant increasers, while the species they protect are usually competitive decreasers (Fig. 1); ruderal species likely do not benefit from facilitation due to sensitivity to competition (Michalet et al. 2006).

The presence of herbivores can alter interactions between unpalatable and palatable species, with facilitative interactions expected when herbivores are present and competition expected in the absence of herbivores (Callaway et al. 2005). The intensity of grazing may also play a role in determining whether positive interactions occur between unpalatable and palatable species. Grazing must have a negative effect on the palatable species so that protection from the unpalatable plant outweighs competitive effects of being near the unpalatable. Rebollo et al. (2005) found that interactions between the biotic refuge, *Opuntia* sp. and the palatable species, *Bouteloua gracilis* were negative in lightly grazed areas while they became positive in intensely grazed areas. Other studies have found that in intensely grazed situations, unpalatable plants lose their ability to function as a refuge and have

observed highest facilitative intensity at intermediate levels of grazing (Brooker et al. 2006; Graff et al. 2007; Smit et al. 2007). Of the few studies that have assessed plant interactions along stress gradients, most have only been able to compare two (high versus low) points along the gradient (Brooker et al. 2006, 2008). More studies are needed that sample entire stress gradients (Brooker et al. 2006; Michalet et al. 2006; le Roux and McGeoch 2010).

We examined relationships between grazing and biotic refuges in highly productive wetland ecosystems in south-central Florida, where cattle ranching is the dominant land use. There are many isolated seasonal wetlands embedded within cattle ranches in this region, and many of these wetlands become invaded by the native tussock-forming rush, *Juncus effusus* L.var. *solutus* Fernald and Wiegand, under high grazing pressure (Boughton et al. 2010). *Juncus* is unpalatable to cattle (Humphrey and Patterson 2000), and we observed many species growing within its tussock in grazed wetlands. Wetlands were randomly selected across the entire ranch and were embedded in areas that received differing levels of grazing intensity, enabling us to examine interactions with *Juncus* across a grazing intensity gradient. In a transplant experiment, we demonstrated that *Juncus* provided refuge for three species (Boughton 2009), providing evidence that *Juncus* is refuge from grazing to some plant species in these wetland communities. However, it has been demonstrated that plant interactions may not always

translate into population or community composition effects (Brooker et al. 2006). Understanding community level effects is important for assessing responses to grazing and may be applicable to forming restoration or management recommendations.

The central goals of this study were to determine if *Juncus* preserves functional diversity in wetlands embedded in subtropical pastures, and to examine how *Juncus* influences the composition of grazed wetland communities. We tested the following hypotheses: (1) species richness and abundance of different response groups (specifically increasers and decreasers) differ between non-*Juncus* and *Juncus* plots, (2) *Juncus* would have significant effects on community composition, and (3) the effects of *Juncus* on other species would change across the grazing gradient.

Methods

This experiment was conducted at the MacArthur Agro-Ecology Research Center (MAERC), a division of Archbold Expeditions, located in south-central Florida (27°09'N, 81°11'W). MAERC is located at Buck Island Ranch, a 4290-ha commercial cattle ranch which is a combination of improved (IMP) and semi-native pastures (SNP) with approximately 630 isolated, seasonal wetlands embedded throughout the property. Approximately half of the land area of Buck Island Ranch is occupied by intensely managed IMP and the other half is occupied by less intensely managed SNP. Improved pastures are composed primarily of Bahia grass (*Paspalum notatum* Flueggé) an introduced forage grass, are fertilized annually with N ($\sim 52 \text{ kg ha}^{-1}$), were historically fertilized with NPK fertilizer (1960s–1986), and are periodically (3–5 year) limed. SNP are composed of a mixture of *P. notatum* as well as native grasses (i.e., *Andropogon* spp. L., *Axonopus* spp. P.Beauv., and *Panicum* spp. Schult.) and have never been fertilized or limed. The climate is subtropical with a mean annual temperature of 22°C, and summer maximums of 33°C. Mean annual precipitation is 1300 mm, of which 69% falls during the wet season (June–October). Cattle are the main herbivore in this system, but feral pigs also are present and often create large soil disturbances in and around wetlands. In a separate study, peak standing biomass in fenced wetlands was $\sim 720 \pm 378 \text{ g/m}^2$ in IMP wetlands and $\sim 400 \pm 185 \text{ g/m}^2$ in semi-native

wetlands (Bohlen and Quintana-Ascencio, unpublished data). In grazed wetlands peak standing biomass was $\sim 345 \pm 172 \text{ g/m}^2$ in IMP wetlands and $\sim 280 \pm 76 \text{ g/m}^2$ in SNP.

We selected 16 wetlands across Buck Island Ranch to sample a range of grazing intensities across SNP and IMP. Grazing intensity varies across the ranch, although IMPs usually experience higher grazing pressure than SNPs. For the duration of this study, which covered two wet seasons, (\sim July 2006–December 2007), average stocking rate was 1.08 cows/ha in IMPs and 0.59 cows/ha in SNPs. However, the IMP and SNP are subdivided into several smaller pastures by fences, and there is a wide range of grazing intensities among pastures within these two pasture-types. Grazing pressure during this study ranged from 0.57 to 1.7 cows/ha in IMPs and from 0.15 to 1.12 cows/ha in SNPs. We used the grazing intensity within the smaller pastures as a proxy for grazing intensity for wetlands within that pasture. Although these values provide a relative measure of grazing intensity within a pasture, local differences in grazing intensity can occur and even in a lightly stocked pasture, grazing pressure can be intense in some areas (Rebollo et al. 2005). Therefore, we evaluated an alternative estimate of local grazing intensity for each study wetland; we measured six heights of the sward within each wetland and averaged them. The use of sward structure to estimate grazing intensity has been recommended because of the heterogeneous nature of livestock grazing (McIntyre et al. 2003). We expected a negative association between vegetation height and grazing intensity. This local measure of grazing intensity was significantly related to cows/ha ($R^2 = 0.40$, $F = 9.3$, $P = 0.009$, $n = 16$).

Experimental design

Our experiment had three factors: pasture (improved versus semi-native), grazing (grazed or ungrazed), and *Juncus* (*Juncus* or no *Juncus*). To insure that study sites were evenly distributed across the ranch property, we divided the property into eight sections and chose one IMP wetland and one SNP wetland randomly within each section for a total of 16 wetlands. Wetlands were chosen for use in the study only if they contained a large population of *Juncus*. At the center of each wetland, two random directions were chosen from eight possible directions (N, NE, E, SE, S, SW, W, and NW).

These locations were used to determine the positioning of two experimental subplots within a wetland. At each experimental subplot we set up a grazed $2\text{ m} \times 2\text{ m}$ plot containing four 1-m^2 quadrats and an adjacent non-grazed $2\text{ m} \times 2\text{ m}$ grazing enclosure containing four 1-m^2 quadrats. Grazing enclosures were constructed with four steel fence posts, four $2.5\text{ m long} \times 1.5\text{ m}$ tall fence panels, and thick wire. Grazing enclosures successfully excluded all large herbivores (i.e., cattle, hogs, and deer) from experimental plots. We constructed 32 enclosures (2 enclosures \times 16 wetlands) for this study. Two of the four $1 \times 1\text{ m}$ subplots within each main grazing treatment plot were randomly assigned the *Juncus* treatment or non-*Juncus* treatment. All *Juncus* plants were removed from the non-*Juncus* treatment quadrats using a machete and large clippers. During the first 2 weeks of the study *Juncus* was kept out of the non-*Juncus* treatment quadrats by repeated clipping. Plots became inundated with water, and other species grew over the space where *Juncus* had been resulting in the death of *Juncus*. No additional resprouting was observed in non-*Juncus* plots during subsequent visits indicating that *Juncus* was completely removed. This experimental setup resulted in four treatments in each wetland: (1) grazed with *Juncus*, (2) grazed without *Juncus*, (3) ungrazed with *Juncus*, and (4) ungrazed without *Juncus*. Community composition of each of these treatments was assessed by categorizing visual estimates of percent cover of each species into seven cover classes (Daubenmire 1959). The visual cover class approach is suitable to use in high density vegetation and for locating rare species. Evidence suggests that cover class estimates are correlated with other methods such as line intercept and point intercept (Kercher et al. 2003). Composition estimates were obtained in September 2006 after all fences and *Juncus* treatments had been established and again in October 2007 at the end of the experiment. Percent cover midpoints of each species from the same treatment per wetland were averaged to remove pseudoreplication (Abrams and Hulbert 1987).

Data analysis

Indicator species analysis in PC-ORD v. 5.32 was used to identify species that were significantly associated with either ungrazed or grazed plots to determine which species increased with grazing (increasers) or decreased with grazing (decreasers).

We used ANOVAs to determine if *Juncus*, grazing, and pasture treatments and their interactions affected species richness and decreaser abundance. Analyses were conducted in SPSS 16.0. Decreaser abundance was logarithmically transformed prior to analysis to better meet test assumptions. We could not approach normality in increaser abundance so we used non-parametric Kruskal–Wallis tests for that variable. We did three Kruskal–Wallis tests, one for each main effect (pasture, *Juncus*, and grazing). We used a Bonferroni correction to determine the correct *P*-value to denote significance ($0.05/3$) which resulted in $\alpha = 0.025$ (Sokal and Rohlf 1995).

To assess the effect of grazing intensity on decreaser cover within *Juncus* clumps, we calculated relative interaction intensity (RII), where $\text{RII} = (B_w - B_o) / (B_w + B_o)$. B_w is decreaser cover with *Juncus* and B_o is decreaser cover without *Juncus*. This index is centered on zero, with positive values indicating facilitation and negative values indicating competition. We analyzed the relationship between RII and grazing intensity (cows/ha and vegetation height) with linear regressions assuming the beta distribution following le Roux and McGeoch (2010) and Smithson and Verkuilen (2006), including pasture-type as a fixed factor.

We analyzed the effect of grazing, *Juncus*, and pasture-type and their interactions on community composition, using non-metric multidimensional scaling (NMS) ordination in PC-ORD v.5.32 with Sørensen distance, a random starting configuration, 50 runs of real data, 100 runs with random data, and 250 iterations. A total of 85 species were included in the ordination. The percent cover of *Juncus* was removed to prevent circularity when comparing treatment effects. Before conducting the ordination we assessed descriptive statistics in PC-ORD of each plot (rows) and found the coefficient of variation was 34.8% indicating no transformations were necessary. Ordination scores were compared between treatments using overlap of 95% CI calculated and graphed in Sigma-Plot v. 10. If confidence intervals did not overlap, treatments were interpreted as significantly different (Callaway et al. 2005).

Community changes were compared among treatments by analyzing the differences in length and direction of successional vectors calculated by comparing composition of individual plots at the beginning and end of the study (McCune and Grace 2002;

McCune 1992). We analyzed vector length and vector direction separately (McCune 1992). Vector length translates into magnitude of change in species composition from the start of the experiment to the end of the experiment (Harcombe et al. 2002), while vector direction represents how similar species composition is between treatments at the end of the experiment. We chose to calculate both vector length and vector direction using city block distances rather than Euclidean distances because city block space gives less weight to outliers (McCune 1992; Harcombe et al. 2002). Standardized vectors were analyzed in a MANOVA in SPSS 16.0 to test whether the heads of the vectors occupy the same region in two-dimensional space with the x and y coordinates of the vector heads as dependent variables and grazing, *Juncus*, and pasture-type as fixed factors. Vector length was analyzed with an ANOVA, with length as the dependent factor and grazing, *Juncus*, and pasture-type and their interactions as fixed factors. Dependent factors were checked for normality and no transformations were necessary.

Results

The results of the indicator species analysis identified the negative association of four species with grazing (decreasers), and the significant positive association of two species with grazing (increasers). Two more species were marginally associated with grazing (Table 1). None of the experimental treatments or their interactions was significant in explaining variation in species richness, although *Juncus* was weakly associated with lower species richness (mean \pm SE, with *Juncus*: 14.03 ± 0.69 , without *Juncus*: 15.78 ± 0.71 , $P < 0.09$, Table 2). As expected, species that were classified as decreasers were significantly less abundant in grazed plots (mean \pm SE: $9.2\% \pm 1.8$) versus ungrazed plots ($37.6\% \pm 3.7$) and in IMP wetlands ($19.9\% \pm 3.6$) compared to SNP wetlands ($26.9\% \pm 3.9$) (Table 3). Decreaser abundance was significantly higher in plots with *Juncus* in grazed areas, but the opposite was true in ungrazed areas (Table 3; Fig. 2). There was a significant pasture-by-grazing interaction in which decreaser species were equally abundant in the ungrazed plots in both pasture-types (IMP: $35.2\% \pm 4.0$; SNP: $39.9\% \pm 4.0$), but decreasers were more abundant in SNP grazed plots

Table 1 Indicator species analysis for decreasers (species that are negatively associated with grazing) and increasers (species that are positively associated with grazing)

	Functional group	Decreaser	Increase	P
<i>Centella asiatica</i>	Native forb	x		0.005
<i>Cynodon dactylon</i>	Exotic grass		x	0.06
<i>Cyperus haspans</i>	Native sedge	x		0.01
<i>Luziola flutans</i>	Native grass		x	0.03
<i>Ludwigia repens</i>	Native forb		x	0.09
<i>P. hemitomon</i>	Native grass	x		0.001
<i>S. striata</i>	Native grass	x		0.004
Bare ground			x	0.001

Four species were negatively associated with grazed plots, while two species were positively associated with grazed plots and two more species were marginally associated with grazed plots (in bold)

Table 2 ANOVA results for species richness among treatments

	df	MS	F	P
<i>Juncus</i> (J)	1	49.0	2.90	0.09
Grazing (G)	1	1.0	0.06	0.81
Pasture (P)	1	27.56	1.63	0.21
J \times G	1	0.56	0.03	0.86
J \times P	1	0.25	0.02	0.90
G \times P	1	0.25	0.02	0.90
J \times G \times P	1	0.56	0.03	0.86
Error	56	16.89		

Table 3 ANOVA results for decreaser abundance among treatments

	df	MS	F	P
<i>Juncus</i> (J)	1	0.62	1.21	0.28
Grazing (G)	1	40.34	78.99	<0.001
Pasture (P)	1	4.97	9.73	0.003
J \times G	1	4.53	8.86	0.004
J \times P	1	0.01	0.01	0.92
G \times P	1	2.76	5.41	0.02
J \times G \times P	1	0.31	0.60	0.44
Error	56	0.51		

Values in bold are significant at $\alpha = 0.05$

($13.8\% \pm 4.0$) compared to IMP grazed plots ($4.7\% \pm 4.0$) (Table 3). This interaction was likely due to lower grazing intensity in SNP wetlands

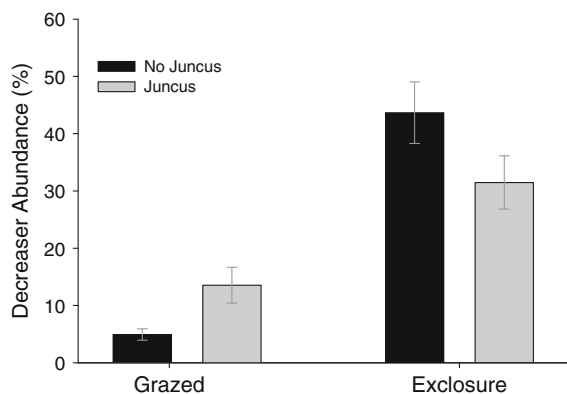


Fig. 2 In grazed plots, decreaser abundance was significantly higher with *Juncus* than without, while the opposite was true in ungrazed plots. This suggests a switch from facilitative to competitive effects of *Juncus* depending on the presence of consumers

compared to IMP wetlands. The coverage of *Juncus* was the same inside the enclosure ($75.5\% \pm 3.4$) and outside the enclosure ($78.9\% \pm 3.4$) at the beginning of the experiment ($df = 1.31$, $F = 0.49$, $P = 0.49$), but was lower inside the enclosures ($50.3\% \pm 4.6$) at the end of the experiment ($df = 1.31$, $F = 4.48$, $P = 0.04$).

Species classified as increasers were significantly higher in grazed areas (mean rank in grazed: 40.88; mean rank in ungrazed: 24.12; $\chi^2 = 13.37$, $P = 0.003$) and higher in IMP wetlands compared to SNP (mean rank in IP: 37.7; mean rank in SNP: 27.3; $\chi^2 = 5.2$, $P = 0.02$). The main effect of *Juncus* was not significant, but there was a trend toward lower mean rank abundance of increasers with *Juncus* (28.6) than without *Juncus* (36.4; $\chi^2 = 2.89$, $P = 0.09$).

In the linear regressions to determine how RII varied along the grazing intensity gradient, we found that both cows/ha ($z = 0.40$, $P = 0.69$) and vegetation height ($z = 0.62$, $P = 0.54$) were unrelated to RII. RII was significantly affected by the grazing treatments, with higher RII values in grazed plots and lower RII values in the exclosures (Fig. 3). Pasture-type had no effect on RII.

Species composition varied among pasture and grazing treatments (Fig. 4). At the beginning of the experiment, there were no major differences between treatments except for a slight pasture effect as indicated by highly overlapping 95% CI among treatments (Fig. 4a). In year two, grazing treatments had a stronger effect on species composition in IMP

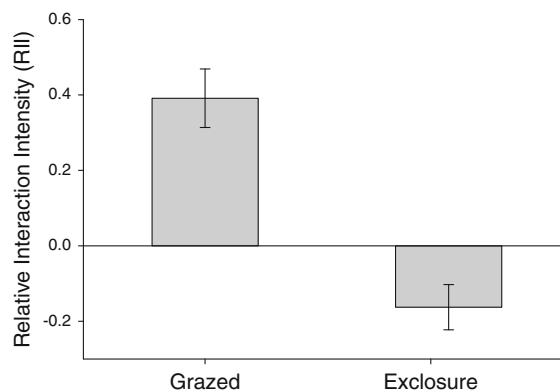


Fig. 3 RII was positive in grazed plots indicating facilitation occurred with *Juncus*, and negative in Exclosure plots indicating competition occurred

wetlands than in SNP wetlands (Fig. 4b). In the ordination, IMP grazed plots were set apart from the other treatments and 95% CI overlapped only one other treatment (Fig. 4b). A three-dimensional solution was selected, and all axes were significant ($P = 0.009$). The percent of variance explained by the entire ordination was 0.66 (Axis 1 $r^2 = 0.22$, Axis 2 $r^2 = 0.21$, Axis 3 $r^2 = 0.22$). Final stress was 18.58 with a final instability of 0.00004. Analysis of the length of successional vectors (rate of vegetation change) showed that the main effect of pasture ($df = 1.63$, $F = 4.92$, $P = 0.03$) was significant, but the main effects of *Juncus* ($df = 1.63$, $F = 1.13$, $P = 0.29$) and grazing ($df = 1.63$, $F = 0.46$, $P = 0.50$) and all interactions were non-significant.

When analyzing vector direction, which represents similarity in species composition between treatments at the end of the experiment, the MANOVA showed the main effect of grazing (Pillai's Trace, $df = 1.63$, $F = 4.95$, $P = 0.01$) was significant while effects of *Juncus* (Pillai's Trace, $df = 1.63$, $F = 0.37$, $P = 0.69$) and pasture (Pillai's Trace, $df = 1.63$, $F = 0.47$, $P = 0.63$) and all interactions were non-significant (Table 4).

As the grazing effect was so strong and may have obscured any effects of *Juncus* on species composition, we ran a second ordination of only the grazed plots to determine if *Juncus* and non-*Juncus* plots differed in vector length and direction. A three-dimensional solution was selected and all axes were significant ($P = 0.019$). The percent of variance explained by the entire ordination was 0.64 (Axis 1 $r^2 = 0.17$, Axis 2

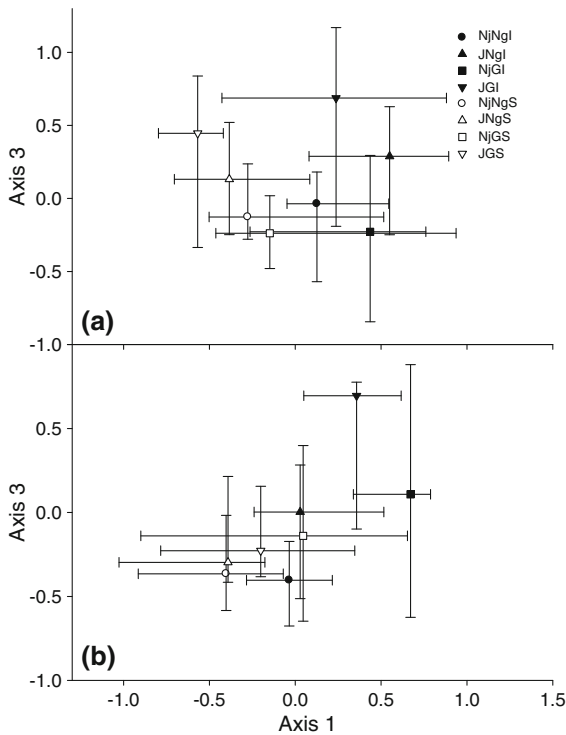


Fig. 4 NMS ordination for the effects of pasture (white = SNP (S), black = IMP (I) and grazing and *Juncus* treatments. Axes 1 and 3 explained the most variation ($r^2 = 0.22$ for each), Axis 2 not shown. Symbols represent the means of eight plots and bars represent 95% CI. **a** Community composition at the beginning of the experiment. **b** Community composition at the end of the experiment. NjNg, non-*Juncus*, non-grazing; JNg, *Juncus*, non-grazing; NjG, non-*Juncus*, grazing; JG, *Juncus*, grazing

$r^2 = 0.21$, Axis 3 $r^2 = 0.26$). Final stress was 17.70 with a final instability of 0.00007. In this analysis, we found that *Juncus* significantly affected vector length ($df = 1.31, F = 10.51, P = 0.003$), with shorter vectors in *Juncus* plots compared to non-*Juncus* plots (Table 4). The MANOVA of vector direction showed

the main effect of *Juncus* (Pillai's Trace, $df = 1.31, F = 4.17, P = 0.02$) was significant while the effect of pasture (Pillai's Trace, $df = 1.31, F = 1.99, P = 0.14$) and their interaction was non-significant (Pillai's Trace, $df = 1.31, F = 0.58, P = 0.63$).

Discussion

Refuge effects of *J. effusus*

The positive effect of *Juncus* on the abundance of grazing-sensitive species (i.e., decreaseers) supports our hypothesis that *Juncus* preserves functional diversity in grazed wetlands. Plots with *Juncus* tussocks were not associated with higher species richness but were associated with higher abundance of decreaseers compared to plots without *Juncus* in a grazed context. Similarly, Oesterheld and Oyarzabal (2004) found that an unpalatable grass provided refuge for a palatable grass preventing the palatable species from becoming locally extinct. Eliminating unpalatable plants, which is sometimes a goal of rangeland managers could result in the eradication of desirable palatable species with consequences for loss of both diversity and ecosystem services (McNaughton 1978; Callaway et al. 2000, 2005; Oesterheld and Oyarzabal 2004).

Although we identified only four species that were significant decreaseers in these wetlands (Table 1), it is likely that a study focused on whole wetlands, rather than on the edge of wetland areas dominated by *Juncus*, would have identified more decreaseer species. Two species that were identified as decreaseers, *Panicum hemitomon* and *Sacciolepis striata*, are native wetland grasses beneficial for both wildlife and as cattle forage. In grazing exclosures, the cover of these decreaseers increased while the cover of *Juncus* cover decreased,

Table 4 SNP wetlands show greater vegetation change (longer vector lengths) over the course of the experiment than IMP wetlands

	SNP	IMP	<i>Juncus</i>	Non- <i>Juncus</i>	Grazed	Ungrazed
Vector length	1.27 ± 0.14	0.89 ± 0.09	1.20 ± 0.14	1.91 ± 0.19	1.14 ± 0.13	1.03 ± 0.12
Vector direction						
Axis 1	-0.32 ± 0.09	-0.19 ± 0.09	-0.26 ± 0.08	-0.25 ± 0.10	-0.15 ± 0.09	-0.36 ± 0.07
Axis 2	0.14 ± 0.09	0.13 ± 0.10	0.08 ± 0.10	0.19 ± 0.09	-0.03 ± 0.10	0.30 ± 0.08

Non-*Juncus* plots show greater vegetation change (longer vector length) than *Juncus* plots. Grazed and ungrazed plots differed significantly in species composition (vector direction) at the end of the experiment. Data are means ± SE. Values in bold represent significant differences between the levels of a factor

suggesting that *Juncus* may be outcompeted by the species it benefits when grazing is removed.

We found no relationship between RII and the sampled grazing gradient. This may be because we were not able to sample a large enough gradient in grazing intensity. In addition, we found no variation in RII between pasture-types. However, we did find that RII was significantly higher in grazed plots compared to ungrazed plots, supporting the notion that facilitation is more prevalent in areas of high consumer pressure (Bertness and Callaway 1994).

Experimental affects of *Juncus*, grazing, and pasture on species composition

The NMS ordination confirmed that species composition of all treatments were similar at the beginning of the experiment indicated by highly overlapping 95% CI, while treatments diverged in species composition at the end of the experiment (Fig. 4). Analysis of successional vectors in the ordination that included the grazing treatments did not show a large effect of *Juncus*.

The vector analysis suggests that there is greater species turnover in SNP wetlands (longer vectors) but relatively stable species composition in IMPs (shorter vectors), which supports our previous findings that IMP wetland plant communities may be niche-assembled while SNP wetlands may be dispersal assembled (Boughton et al. 2010). Since IMP wetlands may represent a stressful environment to some wetland species, due to intense grazing and eutrophication, only species that are tolerant to these conditions can survive there, resulting in a more or less unchanging plant community over time. Harsher environments “filter” out many species, resulting in a smaller pool of species that can persist in these environments, leading to lower beta diversity and increased site-to-site similarity (Chase 2007). Eutrophication and drought have been previously associated with floristic homogenization of plant communities (Chase 2007; Keith et al. 2009).

Grazing was the only factor that significantly distinguished species composition among treatments at the end of the experiment, probably because of the large increase in the relative abundance of decreaser species and a decrease in *Juncus* cover within exclosures. The lack of a strong *Juncus* effect on species composition in the MANOVA may be due to the fact that even though *Juncus* provides protection to

grazing-sensitive species in grazed plots, the cover of the grazing-sensitive species is not maintained to the same level that is observed within exclosures (Fig. 2) and overall the cover of many species is reduced in grazed plots even when *Juncus* is present.

Despite the lack of a strong effect of *Juncus* on species composition across grazing treatments, *Juncus* significantly affected rate of vegetation change and species composition in grazed plots. Lengths of successional vectors were shorter with *Juncus* compared to without *Juncus* suggesting that *Juncus* may have stabilized species composition in grazed conditions. Grazed plots without *Juncus* are not protected from soil trampling and grazing disturbance and this resulted in more species composition change over the course of the study. In addition, because *Juncus* has negative effects on some species due to shading (Ervin and Wetzel 2002) as evidenced by a marginally significant negative effect of *Juncus* on species richness, it may be that only a few species are able to coexist with *Juncus*, thus resulting in less change in composition over the course of the experiment and shorter vector lengths. The second ordination also showed that species composition was different between *Juncus* and non-*Juncus* plots, supporting our result that decreasers were more abundant with *Juncus* than without in grazed plots (Fig. 2).

Implications for management and conservation of wetland plant communities in grazing lands

Changes in the outcomes of plant interactions along ecological stress gradients is interesting from a purely ecological point of view (Bruno et al. 2003), but also has implications for management in ecosystems impacted by human activities (Callaway et al. 2000; Rebollo et al. 2005). Throughout the world, large areas of land are subject to grazing by domestic animals and unpalatable plant species are often present (Brinson and Malvarez 2002; Nicol et al. 2007; Moran et al. 2008). Unpalatable plants interact in various ways with neighboring plants and may serve as sources for recolonization by palatable species when pastures are permitted to recover. By understanding how unpalatable plants function within grazed lands, appropriate management decisions can be made if the goal is to maintain plant communities that provide native forage species, native diversity, and other ecosystem functions.

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