



# Management intensity affects the relationship between non-native and native species in subtropical wetlands

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## Keywords

Biotic resistance; Functional groups; Grasslands; Grazing; Invasion; Land-use; Resource availability

## Nomenclature

Wunderlin (1998)

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## Abstract

**Question:** Does management intensity affect the association between non-native and native species and between non-native species and soil nutrients in wetlands?

**Location:** MacArthur Agro-Ecology Research Center, Florida, USA.

**Methods:** We evaluated native and non-native plant richness and relative frequency in 15 1-m<sup>2</sup> plots in 40 wetlands across two types of pastures, highly managed (fertilized, ditched, planted, heavily grazed by cattle) and semi-natural (unfertilized, lightly seasonally grazed). Plant biomass was collected in five 0.25-m<sup>2</sup> plots per wetland and sorted to species. Soil cores were collected to analyse soil total nitrogen (N) and phosphorus (P). An information-theoretic approach was used to compare mixed effects models considering the association of non-native richness, relative frequency, and biomass with native richness, relative frequency, biomass, C<sub>3</sub> grass relative frequency (a dominant native group), N, P and wetland-type.

**Results:** Non-native richness was negatively correlated with native richness in semi-natural wetlands, but there was no evidence of an association between these variables in highly managed wetlands. Non-native richness increased with increasing soil N in semi-natural wetlands, but not in the highly managed wetlands. Soil P was positively related to non-native frequency in semi-natural wetlands but negatively related in highly managed wetlands. Non-native frequency and biomass were negatively related to relative frequency of C<sub>3</sub> grasses in both management types.

**Conclusions:** Our results indicate that management intensity influences relationships between native and non-native richness. Management intensity interacts with abiotic or biotic factors, such as soil nutrients and composition, in predicting where non-native species will most likely need control.

## Introduction

It is widely recognized that species invasions can cause devastating ecological and economic problems (Vitousek et al. 1997; Mack et al. 2000). Invasions can result in homogenized communities, threatening native flora and altering ecosystem function. Because of the negative impacts of species invasions, much ecological research is focused on understanding factors that promote or prevent invasions. A key area of interest is to examine characteristics that make some communities more susceptible to invasion than others.

The susceptibility of a community to invasion is a function of both abiotic and biotic factors (Davis et al. 2000; Gilbert & Lechowicz 2005; Richardson & Pyšek 2006; Chytrý et al. 2008). Community characteristics such as increased nutrients have been associated with greater exotic richness and invasion (Stohlgren et al. 1998; Kalkhan & Stohlgren 2000; Woo & Zedler 2002; Howard et al. 2004; Matthews et al. 2009) while biotic properties such as high species richness and/or functional diversity have been associated with less invasion (Levine & D'Antonio 1999; Lonsdale 1999; Symstad 2000; Prieur-Richard et al. 2002; Stachowicz et al. 2002; Hooper et al. 2005; Ortega &

Pearson 2005; Huebner & Tobin 2006; Emery 2007; Maron & Marler 2007, 2008; Perelman et al. 2007). In studies of community invasibility, the focus is often on either abiotic or biotic characteristics promoting invasion; however, consensus is growing that when examining community invasibility, both abiotic and biotic factors should be considered simultaneously (Mattingly et al. 2010).

Biotic resistance of a community arises from resident species, which preempt resources and limit invaders from entering the community (Elton 1958). Elton (1958) hypothesized a negative relationship between native and non-native species richness, where species rich communities would be more resistant to invaders because of competition for resources. Biotic resistance has been demonstrated in small-scale experiments where plots with higher species richness were less invasible (e.g. Naeem et al. 2000). At larger spatial scales, however, when greater environmental heterogeneity is encountered, native and non-native richness are often positively correlated because of shared responses to environmental drivers (Ortega & Pearson 2005; Davies et al. 2007; Perelman et al. 2007).

Environmental factors such as nutrient availability, light or disturbance have also been linked to community invasibility (Huenneke et al. 1990; Davis et al. 2000; Howard et al. 2004). Generally, any change in nutrients that results from either direct increases in nutrients (via fertilizer) or from a decrease in uptake by resident species (by disturbance) has the potential to make a community more vulnerable to invasion (Davis et al. 2000). Several studies have found that non-native richness and abundance are positively associated with increased nitrogen (N) concentrations (Stohlgren et al. 1998; Kalkhan & Stohlgren 2000; Howard et al. 2004). Anthropogenic disturbances such as agricultural activities often create environmental conditions that favor non-native species and limit native species. For example, Li & Norland (2001) documented that exotic Brazilian pepper outcompetes native species in enriched abandoned agricultural land within the Florida Everglades. Exotic herbivores, such as cattle, have also been implicated in increases in non-native plant richness because of their role in importing propagules, opening microsites, and damaging resident species (Hobbs & Huenneke 1992).

Intensely managed ecosystems are exposed to a range of disturbances that may be important in promoting non-natives and native ruderals, which are adapted to frequent disturbances (Ortega & Pearson 2005). In less intensely managed ecosystems, which receive little nutrient inputs and have less physical disturbance, resident vegetation is more likely to pre-empt space and other resources from incoming species. Thus, the relationship between native and non-native richness may depend on the disturbance context of the community

(Belote et al. 2008; Lilley & Vellend 2009; Parker et al. 2009). For example, Belote et al. (2008) found that before tree felling disturbance in Appalachian forests, there was no relationship between native and non-native richness at the 1 m<sup>2</sup> scale, whereas after disturbance the relationship between native and non-native richness was positive. The mechanisms by which the disturbance context alters the relationship between natives and non-natives may be related to different population processes occurring in successional versus non-successional (or stable) communities (Compagnoni & Halpern 2009). In successional, frequently disturbed communities, resources are abundant and competitive interactions may be less important, promoting coexistence of natives and non-natives (Belote et al. 2008). In contrast, in less disturbed, stable communities, competition for space and other resources becomes more important for population dynamics resulting in negative relationships between resident species and invaders (Compagnoni & Halpern 2009). Differences in conditions across successional versus stable communities could result in different relationships between invaders and nutrients in the two habitat types. In early successional communities, abundant resources may not be a limiting factor to invasion while in stable communities one would expect nutrients to limit invasion so that positive relationships would be maintained between invaders and nutrients.

Cattle ranching is a dominant land-use in the Northern Everglades region of Florida, and pastures in this region are dotted with small (1 ha or less), ephemeral wetlands. Wetlands in highly managed pastures have low native richness and high exotic plant richness, while wetlands in semi-natural pastures have high native plant richness and low exotic richness (Boughton et al. 2009). In this region, highly managed pastures are characterized by regular additions of fertilizer and lime, heavy grazing during the summer wet season, drainage ditches and upland conversion to non-native forage grasses. Semi-natural pastures are not fertilized or limed, and have moderate grazing, less ditching and are composed of mainly native grasses. The range of disturbance and the heterogeneous abiotic and biotic attributes make these wetlands ideal for examining factors that influence susceptibility to invasion. To quantify the level of invasion in wetlands (~1 ha), we examined several common measures of invasibility including, non-native species richness, relative frequency, and biomass (Stohlgren et al. 1999; Allen et al. 2009; Ricotta et al. 2010).

In this study, we asked if the relationships of (1) non-native and native species, and (2) non-native species and soil nutrients differed depending on management intensity. We expected in highly managed wetlands that the relationships between natives and non-natives would be positive due to increased disturbance promoting

coexistence, while in semi-natural wetlands, the relationship between native and non-natives would be negative. A negative relationship between natives and non-natives would be in line with the hypothesis that resident species pre-empt resources and limit invaders. We expected that the relationship between non-native species and nutrients would be less important in highly managed wetlands than in less disturbed semi-natural wetlands. By incorporating direct measurements of wetland nutrient status along with the wetland type (highly managed or semi-natural) we examined if there were any residual differences between wetland types after removing the effect of nutrient level. If, after accounting for nutrients, there was still an effect of wetland type, this would suggest that disturbances other than nutrient enrichment affect the prevalence of non-native species.

## Methods

### Study area

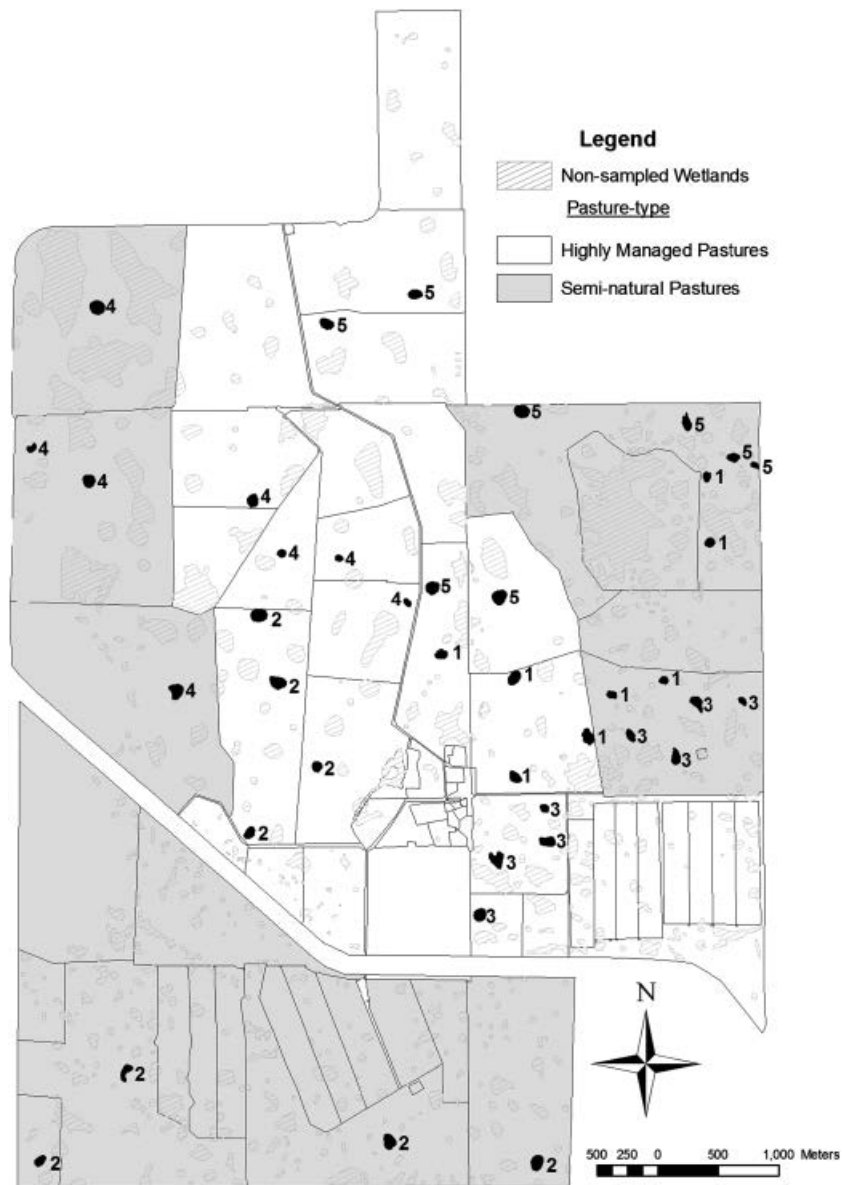
This study was conducted at the MacArthur Agro-Ecology Research Center, a division of Archbold Expeditions, located in south-central Florida (27°09' N, 81°11' W). The climate is humid subtropical with ~130 cm of rainfall per year with a distinct summer wet season and winter dry season. The Center is located within Buck Island Ranch, a 4170 ha commercial cattle ranch, which consists of approximately 50% each of highly managed and semi-natural pastures with approximately 600 isolated, seasonally flooded wetlands (freshwater marshes) (Fig. 1). Soils at the site consist of poorly drained sands with highly managed pastures occurring on better drained Spodosols and Inceptisols and semi-natural pastures occurring on lower-lying Alfisols. Highly managed pastures historically were dry prairie and have been agronomically improved since the 1940s by the annual addition of lime and fertilizer (~1940 to present, 52 kg ha<sup>-1</sup> N; ~1940–1987, ~18 kg P ha<sup>-1</sup>), intensive drainage ditches, and the sowing of the introduced forage grass, *Paspalum notatum* Fluegg. Semi-natural pastures are wet prairie savannas with the natural vegetation mostly intact, which are dominated by native grasses (i.e. *Andropogon* spp. L., *Axonopus* spp. P. Beauv., and *Panicum* spp. Torr.), and have never been fertilized. These areas were originally mixed marsh, wet-prairie systems, which are currently drier than they were historically as a result of large-scale regional drainage projects dating back to the 1950s. These semi-natural pastures have fewer drainage ditches and lower intensity grazing than the highly managed pastures. Both pasture types historically contained small, isolated wetlands, which are still present and are the focus for this study. The land has been used for cattle production

since the 1920s. During the study (2005–2008) the average stocking rate was 0.51 animal units (AU) × ha<sup>-1</sup> in highly managed pastures and 0.28 AU × ha<sup>-1</sup> in semi-natural pastures.

### Wetland selection and plant sampling

Forty wetlands were selected randomly and stratified by pasture-type. Wetland characteristics varied through the study area, so that blocks were used to account for this variation and to approach maximum interspersion of the study wetlands. Each block was spatially stratified and contained eight wetlands (four highly managed and four semi-natural; Fig. 1). Wetlands were selected to be similar in size (~1 ha), shape and hydroperiod. Vegetation sampling was conducted at the end of the growing season in Oct–Nov 2006, at a period of peak biomass. Using ArcGIS 9.3.1 (2009), we selected 15 random points within each wetland to sample species richness in 1 m<sup>2</sup> circular plots. To ensure equal sampling over the entire pond, these 15 points were stratified by five equal area locations within each pond: center, northeast, northwest, southeast and southwest. Five of the 15 points (one in each of the five regions of the pond) were randomly selected for biomass collection. The five biomass points were marked with a steel fence post in order to revisit the plot during subsequent sampling events. Biomass was collected by species within a 0.25 m<sup>2</sup> circular plot. Plants were cut at approximately 10 cm from ground level and a smaller circular plot (0.0625 m<sup>2</sup>) was used to sample below 10 cm. Individual species were bagged and oven dried (70 °C for 48 h) and then weighed. Voucher specimens were collected for most species and deposited in the herbaria at MAERC and the University of Central Florida. A Trimble GPS was used to locate sampling points in the field.

We observed 10 non-native plants in this system for which there is no evidence of direct human intervention to account for their presence in our wetlands, including *Alternanthera philoxeroides* (Mart.) Griseb. (S. America), *Cuphea carthagenensis* (Jacq. J.F. Macbr. (S. America), *Cynodon dactylon* (L.) Pers. (S. Africa), *Eichhornia crassipes* (Martius) Solms-Laubach (S. America), *Hymenachne amplexicaulis* (Rudge) Nees (S. America), *Ludwigia peruviana* (L.) H. Hara (S. America), *Panicum repens* L. (Australia), *Paspalum acuminatum* Raddi (S. America), *Paspalum urvillei* Steud. (S. America) and *Solanum viarum* Dunal (S. America). *Cynodon dactylon*, *H. amplexicaulis*, and *P. urvillei* were originally introduced as forage grasses but were included in our analyses because these grasses are known to spread through water ways, by endozoochory, or wind and do not rely on human activities for movement (Diaz et al. 2003; Newman et al. 2003; Shiponeni & Milton 2006). We excluded exotic



**Fig. 1.** Map of the study site, MacArthur Agro-Ecology Research Center (MAERC) in Florida, USA. Wetlands are depicted with numbers denoting the five experimental blocks.

forage grasses that were planted into our pastures from the non-native species richness counts because these were not considered invasions as the species did not arrive by their own accord; these exotic grasses included *Paspalum notatum* and *Hemarthria altissima* (Poir.) Stapf & C.E. Hubbard.

#### Soil collection and nutrient analysis

At each of the five vegetation biomass sampling posts, two soil samples were collected 1 m from the post in two randomly selected compass directions and aggregated into one sample for a total of five soil samples per pond.

Soil was collected with a hammer core to a depth of 15 cm. Samples were oven dried at 105 °C for 24 h and pushed through a 2 mm sieve. Soil organic matter was measured by loss on ignition using 0.5 g of soil ashed at 450 °C for 16 h. Ash was analyzed for total P (Allen et al. 1974) using the method of Murphy & Riley (1962) on a Technicon Autoanalyzer II (USEPA 1983). Total N was analysed at the Analytical Chemistry Laboratory at the University of Georgia, USA. The Micro-Dumas combustion technique was used and samples were analysed on a Carlo Erba NA 1500 CHN Analyser (Carlo Erba, Chaussée du Vexin, 27 106 Val de Reuil, France).

Analysis of variance was used to determine if N or P differed between pasture-types.

### Statistical analysis

Richness was a pooled count derived across the 15 plots sampled in each wetland. Frequency was defined as the number of occurrences of non-native or native species within the 15 sampled plots. Biomass ( $\text{g m}^{-2}$ ) of species were summed across the five 0.25 m<sup>2</sup> plots to obtain an estimate by wetland. Biomass per wetland was summed for all non-native species and all native species to obtain total non-native biomass and total native biomass, respectively.

We sorted native species into functional groups (defined below) and determined if non-native species richness was related to any of these functional groups using linear regressions. Native species were divided into growth form groups: submergent/emergent, forb (dicotyledonous herbs, including legumes), grass (all species in *Poaceae*, as well as sedges, rushes, and other monocots), shrubs, and ferns. We were not able to identify a few plants that were excluded from the analysis (a maximum of two per wetland, a total of seven unknowns out of 154 species). Grasses were noted as annuals or perennials and by photosynthetic pathway ( $C_3$  or  $C_4$ ). Photosynthetic pathway information was obtained from the relevant literature (Downton 1975; Waller & Lewis 1979; Bowes 1993; Looney et al. 1993). There was a total of 10 different possible functional groups for the native species present at this site: submergent (Sub,  $n=12$ ), annual forbs (AF,  $n=13$ ), perennial forbs (PF,  $n=30$ ),  $C_3$  annual grasses (AG3,  $n=1$ ),  $C_3$  perennial grasses (PG3,  $n=30$ ),  $C_4$  annual grasses (AG4,  $n=1$ ),  $C_4$  perennial grasses (PG4,  $n=25$ ), ferns (F,  $n=3$ ), and shrubs (S,  $n=8$ ). To obtain the relative frequency values for each of these groups, we totaled the number of occurrences for each group (number of times encountered in each of the 15 species composition plots) and then divided this sum by the total number of occurrences of all groups in the whole wetland. In these analyses, relative frequencies were used because this measure was a good reflection of how widely distributed these species were relative to other groups in a wetland. Analysis of variance with relative frequency as the response and wetland type as the predictor was used to determine if functional groups differed between wetland types. Groups with only one species were not included in the analyses.

Multiple models were evaluated using linear regressions utilizing residual maximum likelihood (REML) estimation to assess the associations between exotic species attributes (richness, frequency and biomass, respectively), pasture (fixed factor) and several covariates (native richness,  $C_3$  grasses, total P and total N). We treated the blocks as random effects. We used REML in

order to account for possible unbalanced designs resulting from the lack of control of the range of the covariates (SAS PROC MIXED; Rencher & Schaalje 2008).

Covariates (native richness,  $C_3$  grasses, total P and total N) were centered and scaled by their means and variances, respectively, before model fitting to better assess their effects on exotic species relative to one another. This standardization allows for the comparison among the resulting standardized regression coefficients when the regression variables have different units of measure (see Section 7.5 of Neter et al. 1996).

We evaluated models that corresponded to our hypothesis that relationships between variables would differ between wetland types and which included the interaction of the covariates with wetland type. Models were fitted that considered wetland type plus each covariate and its interaction with wetland type (four possible), and all possible pairs of covariates and their two-way interactions with wetland type (six possible). Using  $\alpha=0.05$  for each test, the highest order terms that were not significant were eliminated from the models. To determine the most informative model of the 10 reduced candidate models we used Akaike Information Criterion corrected for small sample sizes ( $AIC_c$ ; Hurvich & Tsai 1989; Burnham & Anderson 2002). We conducted statistical analyses using procedure GLIMMIX in SAS software version 9.1 (SAS Institute Inc., Cary, NC, US.).

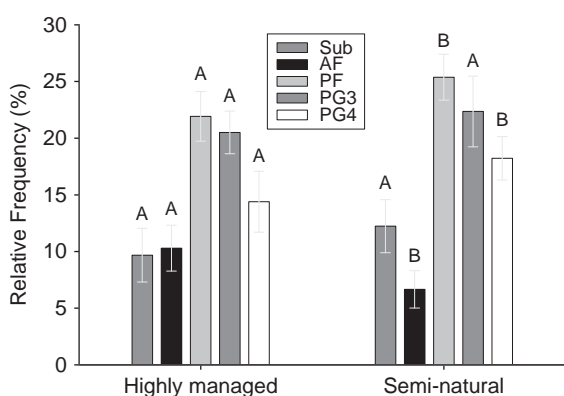
### Results

The species richness and relative frequencies of the functional groups of wetland species differed between management intensities (i.e. highly managed and semi-natural wetland types). The highly managed wetlands had lower native richness and higher non-native richness and non-native biomass than the semi-natural wetlands. The relative frequency of  $C_3$  grasses and native biomass were similar between wetland types (Table 1); however, wetlands of the two types differed in the relative contribution of other functional groups, with highly managed wetlands containing more annual forbs and fewer perennial forbs and  $C_4$  grasses than semi-natural wetlands (Fig. 2). Non-native richness was negatively correlated with the relative frequency of native  $C_3$  perennial grass and native shrubs (Table 2); however, shrubs did not hold explanatory power when present in the same analysis as  $C_3$  grasses and was therefore eliminated in the main models of the  $AIC_c$  analysis (Table 3).

Total soil nutrients did not differ significantly between wetlands of the two management types. Phosphorus (P) tended to be higher in highly managed wetlands, but variances were large and thus no significant differences were detected (Table 1). Levene's test for homogeneity of

**Table 1.** Means  $\pm$  SE of attributes of highly managed and semi-natural wetlands in the MacArthur Agro-Ecology Research Center, Florida, USA. \*Denotes differences between pasture type at 0.05 significance level.

	Highly managed wetlands	Semi-natural wetlands
Sample size	20	20
Area (ha)	0.83 $\pm$ 0.07	0.71 $\pm$ 0.07
Native richness*	20.2 $\pm$ 1.2	30.9 $\pm$ 2.0
Non-native richness*	4.8 $\pm$ 0.2	2.4 $\pm$ 0.4
Native biomass (g m <sup>-2</sup> )	479.9 $\pm$ 81.8	449.5 $\pm$ 46.4
Non-native biomass (g m <sup>-2</sup> )*	146.9 $\pm$ 32.9	41.5 $\pm$ 16.3
C <sub>3</sub> Perennial grass (%)	20.5 $\pm$ 0.9	22.4 $\pm$ 1.5
Soil total phosphorus (ppm)	162.5 $\pm$ 23.6	126.1 $\pm$ 14.9
Soil total nitrogen (ppm)	357.0 $\pm$ 9.6	371.9 $\pm$ 6.9



**Fig. 2.** Relative frequencies of native functional groups in highly managed wetlands and semi-natural wetlands in the MacArthur Agro-Ecology Research Center, Florida, USA. Letters denote significant differences in percent covers between wetland-types ( $\alpha = 0.05$ ). Means  $\pm$  95% CI shown. Sub = Submergent, AF = annual forbs, PF = perennial forbs, PG3 = perennial C<sub>3</sub> grasses, PG4 = perennial C<sub>4</sub> grasses. Relative frequencies of submergent vegetation and perennial C<sub>3</sub> grasses were not different between wetland-types while remaining groups were different.

**Table 2.** Linear regressions showed that non-native species richness was negatively correlated with relative frequency of both C<sub>3</sub> grasses and shrubs in the MacArthur Agro-Ecology Research Center, Florida, USA.

Functional Group	R <sup>2</sup>	F	P
Submergent	0.01	1.57	0.22
Annual forbs	0.05	3.06	0.09
Perennial forbs	0.03	2.16	0.15
C <sub>3</sub> Grasses	0.33	18.31	< 0.001
C <sub>4</sub> Grasses	0.05	1.99	0.17
Ferns	0.00	0.37	0.54
Shrubs	0.29	15.53	< 0.001

variances showed that variance was no different between the two wetland types for both total P ( $F = 0.26$ ,  $P = 0.61$ ) and total N ( $F = 0.045$ ,  $P = 0.83$ ). Total soil N also did not differ between wetland types and the results did not differ

**Table 3.** Reduced models for non-native richness, non-native frequency, and non-native biomass and associated Akaike information criterion (AIC<sub>C</sub>). AIC<sub>C</sub> = Akaike Information Criterion corrected for small sample sizes,  $\Delta_i$  = difference between the lowest AIC<sub>C</sub> and AIC<sub>C*i*</sub>,  $w_i$  = model weight given the data.

Models for non-native richness	AIC <sub>C</sub>	$\Delta_i$	$w_i$
Wetland type (WT)+total nitrogen (N)+WT $\times$ N	139.0	15.7	0.17
Wetland type+native richness (NR)+WT $\times$ NR	134.3	11	0.22
Wetland type+C <sub>3</sub> grass	134.2	10.9	0.22
WT+native richness (NR)+ total N	123.3	0	0.38
(N)+WT $\times$ NR+WT $\times$ N			
Models for non-native relative frequency			
WT+total nitrogen	266.1	14.8	0.17
WT+C <sub>3</sub> grass	261.9	10.6	0.21
WT+total phosphorus (P)+ total N	259.7	8.4	0.24
WT+C <sub>3</sub> grass+ total P (P)+WT $\times$ P	251.3	0	0.37
Models for non-native biomass			
WT+C <sub>3</sub> grass	465.8		

after the removal of two outliers in the highly managed wetlands (Table 1).

The relationship between non-native richness with native richness varied markedly between wetland types (Table 4, Fig. 3). Specifically, non-native richness decreased with native richness in semi-natural wetlands (coefficient =  $-1.11$ ; Table 4) but was not significantly related to native richness in highly managed wetlands (coefficient =  $0.18$ ). Non-native richness increased with increasing soil N in semi-natural wetlands (coefficient =  $1.14$ ), but there was no evidence of this relationship for the highly managed wetlands (coefficient =  $0.22$ ; Table 4, Fig. 4). An analysis conducted without two outliers in the highly managed wetlands produced consistent results.

The correlation between non-native frequency and soil P varied between wetland types with a negative relationship in highly managed wetlands (coefficient =  $-1.37$ ) and a positive relationship in semi-natural wetlands (coefficient =  $4.18$ ) (Table 5, Fig. 5).

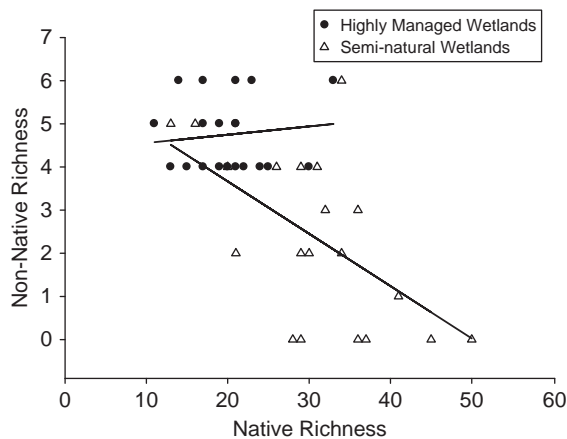
There was a negative relationship between C<sub>3</sub> grasses and non-native species richness (coefficient =  $-0.91$ ,  $F = 28.94$ ,  $P < 0.0001$ ), non-native frequency (coefficient =  $-4.69$ ,  $F = 17.06$ ,  $P = 0.0003$ ), and non-native biomass (coefficient =  $-42.8$ ,  $F = 5.15$ ,  $P = 0.03$ ) in both wetland types.

## Discussion

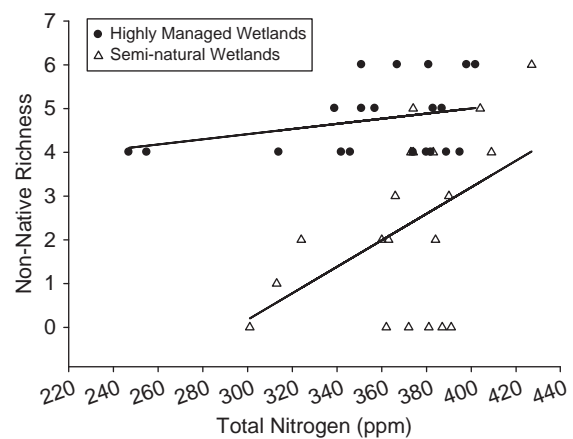
Knowledge of the resource and competitive environments are two of several essential components necessary to understand why particular communities become invaded (Gilbert & Lechowicz 2005). Our results indicate that highly managed wetlands compared with semi-natural wetlands have: (1) higher exotic species richness and lower native species richness; (2) higher frequency of

**Table 4.** Results of the best model (identified by AIC<sub>c</sub>) describing non-native richness. Results were obtained using linear regressions utilizing restricted maximum likelihood (REML) estimation. Note that the algebraic sum of the coefficient of the semi-natural wetlands for native richness (NR) and the coefficient of NR × wetland management type interaction estimates the coefficient of the highly managed wetlands for NR. The coefficient for highly managed wetlands for nitrogen was estimated in the same way. The fixed variation accounted for by the mixed model was R<sup>2</sup> = 0.70.

Source of variation	Wetland type	Coefficient	SE	t	P
Intercept	Highly managed	2.13+2.77 = 4.90	0.41	12.04	0.0001
	Semi-natural	2.77	0.35	7.96	0.0014
Native Richness (NR)	Highly managed	1.29 - 1.11 = 0.18	0.42	0.41	0.6827
	Semi-natural	- 1.11	0.25	- 4.45	0.0001
Nitrogen	Highly managed	- 0.92+1.14 = 0.22	0.22	1.01	0.3214
	Semi-natural	1.14	0.31	3.70	0.0009



**Fig. 3.** The relationship between native and non-native species richness varied by wetland-type, with a negative relationship in semi-natural wetlands and a non-significant positive relationship in highly managed wetlands (slopes: Semi-natural = - 1.11; Highly managed = 0.18). The fixed variation accounted for by the mixed model was R<sup>2</sup> = 0.70 (see Table 4).



**Fig. 4.** In both wetland-types of the MacArthur Agro-Ecology Research Center, Florida, total nitrogen was positively related to non-native richness; however, the slope of the relationship in semi-natural wetlands (1.14) was much steeper than that in highly managed wetlands (0.22; not statistically significant). The fixed variation accounted for by the mixed model was R<sup>2</sup> = 0.70 (see Table 4).

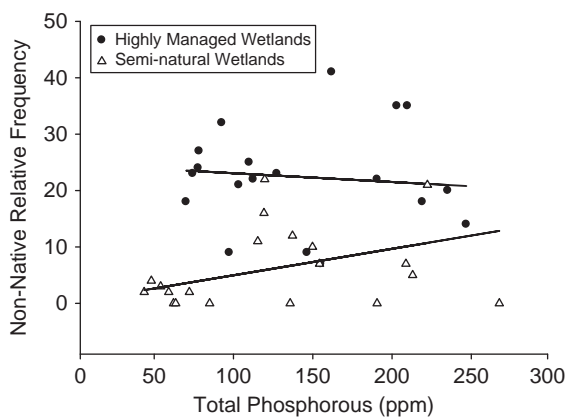
annual forbs and lower frequency of perennial forbs and C<sub>4</sub> grasses; and (3) different relationships between non-native and native richness, and non-native richness and soil nutrient content. In highly managed wetlands there was no evidence of an association between native and non-native richness while in semi-natural wetlands, this relationship was negative. Furthermore, correlations between non-native richness and native richness and between non-native richness, frequency and soil nutrients were often more pronounced in semi-natural wetlands.

An observed negative relationship between native richness and non-native richness has been explained by several mechanisms. One explanation is biotic resistance, which arises from resident species pre-empting resources and limiting invaders from entering a community (Elton 1958). Alternatively, a negative relationship could indicate that highly invaded wetlands have low native richness because of negative invader effects (Levine &

D’Antonio 1999; Ortega & Pearson 2005); however, the validity of this alternative hypothesis is dependent on the presence of strong invaders (Ortega & Pearson 2005). In our system, only 10 non-native species are present and none of them can be classified as strong invaders because they do not readily form monocultures in these grazed, ephemeral wetlands. Another alternative hypothesis is that natives and non-natives are responding oppositely to extrinsic drivers (Lilley & Vellend 2009). For example, cattle grazing intensity could have played a role in generating the negative relationship between native and non-native richness because grazing could be negatively correlated with native diversity and positively correlated with non-native species diversity (McIntyre & Lavorel 1994; Rusch & Oesterheld 1997; Diaz et al. 2007); however, native richness was weakly positively related (R<sup>2</sup> = 0.19, P = 0.05, n = 20; unpublished data) and non-native richness was unrelated to soil bulk density, a proxy for grazing intensity (Greenwood

**Table 5.** Results from the linear regression utilizing restricted maximum likelihood (REML) estimation of the best model of non-native frequency. Note that coefficient for highly managed type was estimated from the algebraic sum of the semi-natural type coefficient for total phosphorus and the coefficient value for the interaction of total phosphorus with management. The fixed variation accounted for by the mixed model was  $R^2 = 0.67$ .

Source of variation	Wetland type	Coefficient	SE	t	P
Intercept	Highly managed	$13.77 + 7.83 = 21.60$	1.63	13.23	0.0001
	Semi-natural	7.83	1.67	4.68	0.0095
C <sub>3</sub> Grass Phosphorus	Highly managed	$-4.69$	1.13	$-4.13$	0.0003
	Semi-natural	$-5.55 + 4.18 = -1.37$	1.29	13.23	0.0001
		4.18	2.03	2.06	0.0480



**Fig. 5.** The relationship between total phosphorus and non-native frequency varied by wetland-type, with a positive relationship in semi-natural wetlands and a weakly negative relationship in highly managed wetlands (slopes: Semi-natural = 4.18; Highly managed =  $-1.37$ ). The fixed variation accounted for by the mixed model was  $R^2 = 0.67$  (see Table 5).

& McKenzie 2001; Tate et al. 2004; Manier & Hobbs 2007) suggesting that a cattle grazing gradient was not the underlying cause for the negative relationship between non-native and native richness.

The lack of association observed between native and non-native richness in more intensely disturbed wetlands suggests that nutrient additions, intense cattle grazing and increased soil disturbance may support the coexistence of native and non-native species. In this habitat, native ruderals and non-natives may be responding positively to physical disturbance and enriched soils (Levine 2000; Naeem et al. 2000). There was a higher relative frequency of annual native forbs in wetlands in highly managed pastures compared with wetlands in semi-natural pastures (Fig. 2) suggesting a positive response of native ruderals to conditions in the more disturbed wetlands. Similarly, in successional forests, ruderal natives and non-natives were found to respond similarly to factors that promote colonization, such as exposure of mineral soil (Compagnoni & Halpern 2009).

Increased soil N was associated with increased richness of non-native species in semi-natural wetlands, but our

data does not provide evidence of this relationship in highly managed wetlands. The positive relationship of N and non-native richness in semi-natural wetlands may indicate that exotic species are responding favorably to increased nutrients, as found in other studies (Stohlgren et al. 1998; Kalkhan & Stohlgren 2000; Howard et al. 2004). The absence of a relationship between exotics and N in highly managed wetlands may indicate that the relationship becomes less important as exotic species become more abundant in an area (Wiser et al. 1998) or that species are less N-limited in highly managed wetlands. Our analysis also showed that there was a significant effect of both N and wetland type on non-native richness with highly managed wetlands containing greater richness and biomass of non-native species. This relationship suggests both nutrient level and other disturbances affect the prevalence of exotics in highly managed wetlands. For example, the intensity of ditching, which varies between the two pasture types could have a large effect on non-native richness because of the possible role of ditches in seed and propagule dispersal. In addition, increased cattle activity near certain wetlands may lead to increases in non-native species. In combination, density of ditching and variable cattle activity could lead to a gradient of non-native propagule pressure across the landscape and result in different exposure rates of exotics for particular wetlands.

The relationship of soil P and non-native frequency differed between wetland types. Soil P was positively related to frequency of non-natives in semi-natural wetlands but weakly negatively related in highly managed wetlands. In general, soils with increased nutrients are expected to directly benefit fast-growing, non-native species (Davis et al. 2000). Soil P is likely associated with increased growth and vigor of the established non-natives leading to higher non-native cover. For example, P was associated with increased cover of non-natives in Californian vernal pools (Gerhardt & Collinge 2003). The negative correlation of P and non-native frequency in highly managed wetlands might suggest that these species are not P limited.

We did not detect any differences in the nutrient content of these two wetland types. This is likely because of complex relationships with soil nutrients and organic



matter that may have varied between wetlands. Other studies on this ranch have found higher levels of P in highly managed wetlands, and this trend is clearer when testing water nutrients (Steinman et al. 2003; Boughton et al. 2009). In addition, Bohlen & Gathumbi (2007) found that the influence of pasture type on N cycling is complex, with highly managed wetlands having reduced soil N cycling compared with semi-natural wetlands owing to negative influences of cattle grazing on organic matter. Semi-natural wetlands had higher nitrate concentrations than highly managed wetlands during the dry season (Bohlen & Gathumbi 2007), which is the season we measured total N in our study. Our results indicate that one soil sampling event to characterize nutrient availability may be insufficient; however, although the average nutrient content did not differ between pasture types, we found that the gradient of nutrient availability covered by the wetlands in our study affected non-native species richness and frequency.

Recently, there has been increased interest in determining which functional groups resist invasion because of the implications for management and restoration (Bakker & Wilson 2004; Funk et al. 2008). In our study the relative frequency of C<sub>3</sub> perennial grass was negatively correlated with non-native richness, frequency and biomass in both semi-natural and highly managed wetlands. As one of the dominant functional groups in our system, C<sub>3</sub> grasses could play a role in reducing wetland invasion by the preemption of resources, but experimental tests would be needed to confirm this conclusion. It is unclear at this point whether some attribute of C<sub>3</sub> grasses *per se* suppresses invaders or if the suppression merely occurs because these grasses are dominant. Dominant species are known to have strong effects on ecosystem processes (McNaughton & Wolf 1970). Alternatively, the negative correlation may represent effects of invaders on C<sub>3</sub> grasses (Ortega & Pearson 2005) or by the opposite responses of C<sub>3</sub> grasses and exotics to extrinsic drivers (Lilley & Vellend 2009). The C<sub>3</sub> grasses negatively correlate with soil N ( $r = -0.63$ ,  $P = 0.003$ , for semi-natural wetlands, and  $r = -0.15$ ,  $P = 0.539$  for highly managed wetlands). Soil N, however, was positively related to non-native species richness. It is therefore plausible that the effects of soil N may be driving the negative relationship of C<sub>3</sub> grasses and non-native richness. Nitrogen fertilization can have negative effects on native species, especially rare species (Suding et al. 2005). Our analysis suggests that C<sub>3</sub> grasses account for as much or more of the variation in non-native frequency and biomass than does soil N. In the analyses of non-native frequency and biomass, whenever C<sub>3</sub> grasses and soil N were included in the same model, the effects of soil N after accounting for C<sub>3</sub> grasses were non-significant while the effects of C<sub>3</sub> grasses after ac-

counting for soil N were significant. This provides support to the idea that one of the dominant groups, C<sub>3</sub> grasses, confers some resistance to non-native proliferation in these wetlands.

In conclusion, we found that relationships between native and non-native richness and between non-native attributes and nutrient availability depended on management intensity. The mechanisms by which management intensity affects invasion dynamics may be related to differences in early successional versus later successional communities. Highly managed wetlands may be early successional with disturbance and ample resources creating conditions where competition for space may be less important. This idea is supported by our findings that soil nutrients were not as strongly correlated with non-native richness and frequency in highly managed wetlands and the lack of a strong relationship between natives and non-natives. In semi-natural wetlands, we observed stronger relationships between non-natives, natives and nutrients, which may reflect the greater importance of nutrient limitation and pre-emption in these less disturbed environments. A better understanding of how management intensity influences invasion as well as how management intensity interacts with abiotic or biotic factors, such as soil nutrients and species composition, can assist land managers in predicting where non-natives species will most likely need control (Diez et al. 2009). Our results suggest that measures to prevent increases in soil nutrients in less disturbed wetlands may help to prevent increases in non-natives in these wetlands and, conversely, that non-native control efforts would be most necessary in wetlands with higher nutrients. In addition, maintaining populations of the dominant native functional group may confer some resistance to invaders in wetlands.

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