Land-use and isolation interact to affect wetland plant assemblages

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Different management regimes imposed on similar habitat types provide opportunities to investigate mechanisms driving community assembly and changes in species composition. We investigated the effect of pasture management on vegetation composition in wetlands with varying spatial isolation on a Florida cattle ranch. We hypothesized that increased pasture management intensity would dampen the expected negative effect of wetland isolation on native species richness due to a change from dispersal-driven community assembly to niche-driven assembly by accentuated environmental tolerance. We used native plant richness, exotic plant richness and mean coefficient of conservatism (CC) to assess wetland plant assemblage composition. Sixty wetlands were sampled, stratified by three levels of isolation across two pasture management intensities; semi-native (less intensely managed; mostly native grasses, never fertilized) and agronomically improved (intensely managed, planted with exotic grasses, and fertilized). Improved pasture wetlands had lower native richness and CC scores, and greater total soil phosphorus and exotic species coverage compared to semi-native pasture wetlands. Increased wetland isolation was significantly associated with decreases in native species richness in semi-native pasture wetlands but not in improved pasture wetlands. Additionally, the species–area relationship was stronger in wetlands in improved pastures than semi-native pastures. Our results indicate that a) native species switch from dispersal-based community assembly in semi-native pastures to a species-sorting process in improved pastures, and b) recently-introduced exotic species already sorted for more intensive management conditions are primarily undergoing dispersal-based community assembly. That land-use may alter the relative importance of assembly processes and that different processes drive native and exotic richness has implications for both ecosystem management and restoration planning.

The conversion of land to agricultural or other human use has reduced wetland area worldwide (Zedler and Kercher 2005) and disrupted natural processes governing species composition and structure (de Blois et al. 2002). Wetlands subject to human activities often have increased nutrients due to surface runoff (Bedford et al. 1999). Typically, disturbed wetlands are smaller and more spatially isolated than less disturbed wetlands because they are more susceptible to manipulation and influence of adjacent land use (Lachance and Lavoie 2004). Because wetlands contribute valued ecosystem services such as maintaining biodiversity, water quality enhancement, flood abatement, and carbon sequestration (Zedler and Kercher 2005), understanding factors that degrade wetland habitat is important relative to assessing alterations in ecosystem services and the development of alternative land use strategies to maintain and maximize benefits of wetlands to humans and wildlife. This is especially crucial on agricultural lands where wetlands could potentially lessen negative impacts of agricultural activities, such as, nutrient export to downstream freshwater ecosystems and decline in native biodiversity.

Aquatic plants are central to wetland functions such as nutrient cycling and habitat structure (Bouchard et al. 2007) and are influenced by management regime and spatial configuration (Lopez and Fennessy 2002). Vegetation composition in many wetland communities is known to shift in response to nutrient inputs from land-use in the resident watershed (Ehrenfeld and Schneider 1991, Cohen et al. 2004), particularly in regard to decreases in native species and increases in non-natives and/or weedy species. Decreased native plant diversity is often attributable to increased productivity associated with eutrophication (Wilson and Keddy 1988, Mountford et al. 1993). Eutrophication of wetlands is a large and continuing problem in Florida where wetlands that were historically low in phosphorus (P) now occupy a significant proportion of the landscape (Qualls and Richardson 1995, Gathumbi et al. 2005, Vymazal et al. 2008).

Effects of wetland spatial configuration on wetland plant assemblages are less well-known but should interact with land-use effects. The theory of island biogeography (MacArthur and Wilson 1967) is potentially valuable for

testing hypotheses about community assembly in isolated wetlands embedded in terrestrial landscapes. The theory predicts that smaller and/or more isolated islands will have fewer species. The species-area relationship has been well-studied in wetlands (Møller and Rørdam 1985, Lopez et al. 2001, Matthews et al. 2005, Houlahan et al. 2006) but effects of isolation on wetland plant species richness remain unclear. Some studies reported negative isolation effects on species richness consistent with island biogeography theory (Lopez et al. 2001, Lopez and Fennessy 2002, Mulhouse and Galatowitsch 2003, Matthews et al. 2005) but others reported no relationship between isolation and wetland plant species richness (Møller and Rørdam 1985, Brose 2001, Wright et al. 2003).

Contrasting results on the effect of isolation on species richness may be due to different techniques for measuring wetland isolation across studies. Commonly used measures of isolation include distance to the nearest wetland or nearest three wetlands; these measures may lack biological relevance for the dispersal of some plant species, particularly those that require localized high density of wetlands as stepping stones for dispersal pathways (Møller and Rørdam 1985). Thus, in some cases, isolation measures have been improved by including wetland density and sizes (Møller and Rørdam 1985). Additionally, the effect of wetland isolation on species richness may depend on land-use type, because environmental conditions can influence community assembly (Chase 2007). Mechanisms potentially influencing community assembly include species' tolerances to environmental conditions and species dispersal driven by stochastic colonization and extinction processes (Chase and Liebold 2003). In harsh environments where disturbance is frequent, species' tolerance limits may drive community composition (Chase and Liebold 2003). In less disturbed habitats, dispersal-driven assembly may become more important as species tolerance limits becomes less vital for survival (Chave 2004). Therefore, wetland isolation may become less significant as land-use management intensifies and local conditions override effects of dispersal limitation.

In this paper we focus on wetland vegetation responses to management intensity of surrounding pastures and to the degree of wetland isolation on a cattle ranch in Florida. Across a gradient of disturbance conditions, we measured native and exotic species richness and mean coefficient of conservatism scores (CC) within depressional wetlands. Wetlands in Florida ranches present an excellent model for examining the effects of P-based eutrophication on wetland plant assemblages because they are embedded in both highly impacted improved pastures (more intense grazing, greater disturbance, high P) and less impacted native or semi-native pastures (less intense grazing, less disturbance, low P) (Gathumbi et al. 2005). They are also an ideal system for examining landscape-level processes because numerous small wetlands are dispersed throughout areas with different land-use intensity. The main purposes of this study were to determine: 1) how land-use intensity (improved vs semi-native pasture-types) influences wetland plant species richness and floristic quality (coefficient of conservatism scores); 2) how wetland size and isolation affect species richness of native and exotic wetland plants, and 3) if the importance of wetland isolation differed between the two land-use intensities.

Specifically, we expected that wetland isolation would predict species richness better in semi-native pasture wetlands than in improved pasture wetlands. Such a result would lend support to the hypothesis that greater disturbance intensity in improved pastures elevates the importance of niche-based community assembly relative to dispersal-based community assembly in semi-native pastures (Chase and Liebold 2003, Chase 2007).

Methods

Site description

This study was conducted at the MacArthur Agro-ecology Research Center, a division of Archbold Expeditions, in south central Florida (27°09′N, 81°11′W). The Center is located at Buck Island Ranch, a 4252-ha commercial cattle ranch with over 600 isolated, seasonal wetlands embedded throughout the property. The wetlands are evenly distributed among intensely managed improved pastures and less intensely managed semi-native pastures (Fig. 1). Improved pastures are composed primarily of the introduced forage grass, Bahia grass *Paspalum notatum*, are typically fertilized annually with N, were historically fertilized with P (1960s–1986), are grazed more intensely during the summer wet season, and contain numerous drainage ditches. Semi-native pastures are composed of a mixture of Bahia grass as well as native grasses (i.e. *Andropogon* spp., *Axonopus* spp., and *Panicum* spp.), have never been fertilized, are moderately grazed mostly during the winter dry season, and have few drainage ditches. During 2005–2008, the average annual stocking rate was 0.52 animal units (AU) ha^{-1} in improved pastures and 0.28 AU ha^{-1} in semi-native pastures (1 AU = 1 cow-calf pair). Cattle use wetlands for forage, drinking water, and cooling and can spend considerable time in wetlands on hot days. Because improved pastures are grazed more heavily than semi-native pastures, it is possible that cows may aid some wetland plants in dispersing among wetlands; however, because we do not have detailed records of cow movements among wetlands, this hypothesis is difficult to test.

In addition to grazing intensity differences between pasture-types, fertilizer regimes differ. Improved pastures are generally fertilized annually with N (~ 50 kg ha^{-1}) and were regularly fertilized with NPK fertilizer (~ 20 kg P ha^{-1}) for over two decades until 1987 (Capece et al. 2007). In 1987, P fertilizer was discontinued though N fertilizer continues to be applied. Because detailed historical and present differences in grazing, fertilizer and soil disturbance were unable to be quantified, we used pasture-type as a categorical variable to incorporate these differences in statistical analyses.

In May–August 2005 we surveyed plant communities in thirty wetlands each in improved pastures and semi-native pastures (n = 60). In addition to wetland isolation and size, we also measured total soil phosphorus and soil pH to determine how these factors relate to wetland vegetation characteristics.
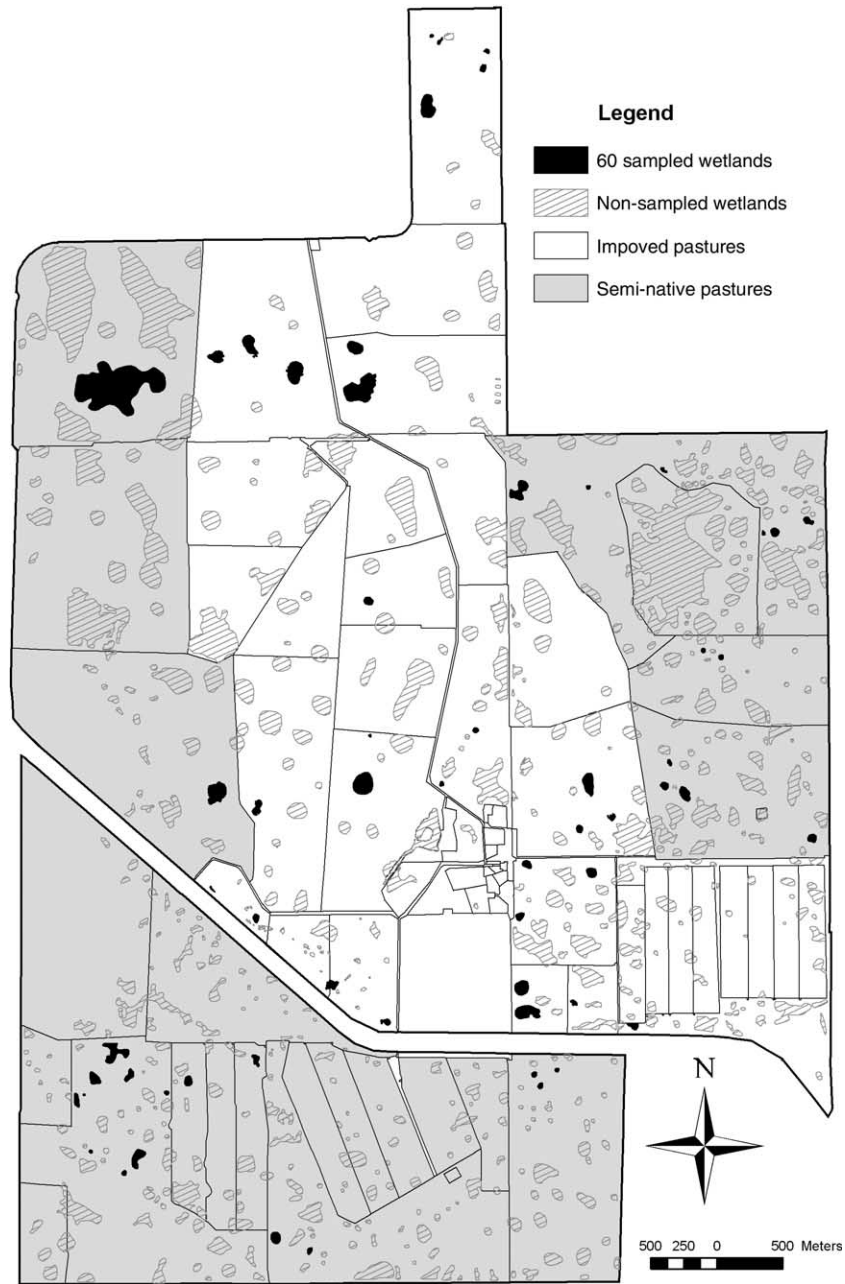
Figure 1. Map of the study area on Buck Island Ranch, the location of MAERC.

Wetland selection

We randomly selected wetlands, first by pasture-type (30 in each type) then by isolation index values (10 in each of three isolation categories per pasture-type). Isolation index was calculated using the equation (Hanski and Thomas 1994):

$$S_i = -\sum_{j}^{n} ((exp(-\alpha d_{ij})) \times A_j) \qquad (1)$$

where d_{ij} is distance (m) from focal patch i to j through n, where n = 628 (total number of wetlands at MAERC), A_j is the area (ha) of the wetland, and α is a constant for strength of distance and area affects; we used $\alpha = 1$ as a conservative

estimate (Quintana-Ascencio and Menges 1996). Three categories of isolation (high, medium, low) were determined using the distribution of isolation scores calculated within a 5000 m^2 radius. Highly isolated wetlands had higher index scores, low isolation had lower scores, and wetlands with scores in the middle of the distribution were classified as having medium isolation. We use the transformation of S_i in graphical representations and analysis for clarity. Because we multiplied by -1 and ln transformed the isolation index, positive correlation of species richness with the transformed isolation index would be expected if isolation negatively affected plant species richness.

To account for the effect of different isolation measures, we also determined distance to the nearest wetland and the

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average distance to the nearest three wetlands. We evaluated scale-dependence of the isolation index (eq. 1) and identified all wetlands within circular buffers around each of the sixty wetlands. Buffer radii (m) were: 100, 200, 300, 400, 500, 1000, 1500, 2000, 2500, and 3000. We then calculated isolation (eq. 1) for each of the central wetlands at each buffer scale. For this analysis, we used National Wetland Inventory maps to include buffer wetlands on neighboring properties. We calculated distances among wetlands based on centroid-to-centroid (c-c), centroid-to-edge (c-e), and edge-to-edge (e-e) for each of the buffer radii. Centroid-to-centroid distances are easier to calculate in GIS than other measures, but we questioned the biological relevance of this measure since it may underestimate the density of wetlands within a particular buffer, considering that wetlands often have irregular shapes and distance between wetland centroids are farther than distances measured between wetland edges. Analyses were conducted with Arc View GIS 9.0. Log transformations were performed on both nearest-neighbor distances and average distance to the nearest three wetlands for analyses. Additionally, c-c isolation indices calculated within radii of 100–600 m and c-e and e-e isolation index values were log transformed to meet normality requirements. After preliminary analyses, we found that edge-to-edge distance in a radius of 400 m was the best fit for a model relating isolation to species richness, explaining 44% ($r^2 = 0.44$, $p < 0.001$) of the variation in species richness in semi-native pasture wetlands. Thus we used this isolation index in all subsequent analyses (Fig. 2). In comparison, distance to the nearest wetland (improved wetlands: $r^2 = 0.158$, $p = 0.030$; semi-native wetlands: $r^2 = 0.141$, $p = 0.041$) and the average distance to the nearest three wetlands (improved wetlands: $r^2 = 0.099$, $p = 0.090$; semi-native wetlands: $r^2 = 0.074$, $p = 0.146$) explained little or no variation in species richness. The key differences between S_i and the simpler measures of isolation are the inclusion of the distal wetland area (A_j) and the aggregation of the distances within the buffer. Therefore, we also looked at the two parts of eq. 1
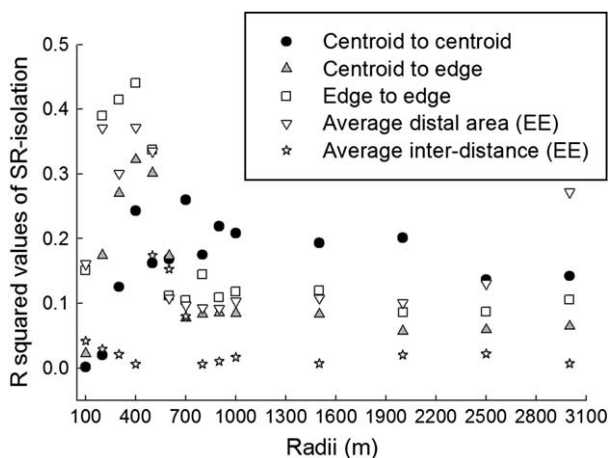

Figure 2. R-square values of the regressions between species richness (SR) and the isolation index calculated within different sizes of buffers (m) around each sampled wetland. Additionally, mean wetland area within buffers (distal area) and mean distance for all wetlands within buffers was calculated and analyzed separately. Semi-native wetlands results only.

(d_{ij} and A_j) and their relationship to species richness separately (Fig. 2). Distal wetland area explained more of the variation in species richness compared to distance between wetlands but the edge to edge isolation index which includes both factors produced a stronger correlation than considering each alone (Fig. 2).

Vegetation sampling

Within each wetland, vegetation was sampled along two transects, beginning at the center and traversing to the edge of the wetland using randomly selected compass directions. Edges of wetlands were determined by sampling until the vegetation cover was >90% pasture grass cover was present. A 1-m^2 quadrat was placed randomly every 5 m along the transect to sample vegetation as percent cover. Transects were used to ensure that all vegetation in deep and shallow zones were sampled. For the 60 sampled wetlands 1005 1 m^2 plots were surveyed. Species nomenclature followed Wunderlin (1998).

We calculated species–area curves and asymptotic estimates of species richness to assess sampling adequacy using PC-ORD v4. Our sampling effort fit within 95% confidence intervals for bootstrap asymptotic estimates of species richness for 58 of 60 wetlands. Also, results did not differ between bootstrap or observed species richness; therefore, we present results from analyses using observed species richness.

In addition to total species richness, we calculated mean coefficient of conservatism (CC) as an index of "quality" of the wetland plant assemblage to account for the presence of exotic and weedy species. The CC score indicates the specificity of a plant species to a particular habitat or tolerance to disturbance intensity (Lopez and Fennessy 2002, Cohen et al. 2004, Matthews et al. 2005). These coefficients range from 0 to 10, where species with a CC = 10 exhibit very limited tolerance to disturbance and a high degree of specificity to ecological conditions, and a CC of zero indicates exotic or opportunistic native taxa (Cohen et al. 2004). We used the average CC score of a wetland plant assemblage as an index of the level of disturbance in the wetland. We selected this metric over the floristic quality assessment index (FQAI; Andreas and Lichvar 1995) because it has been demonstrated to better predict wetland condition and does not emphasize species richness (Lopez and Fennessy 2002, Cohen et al. 2004, Matthews et al. 2005). We calculated the average CC of each wetland as:

$$\bar{C}\bar{C}_j = \sum_{i=1}^{n} CC_{ij}/N_j \qquad (2)$$

where the mean CC_j is the average coefficient of conservatism score for the wetland, and CC_{ij} is the coefficient of conservatism scores of species i through j and N_j is the number of species in the wetland.

Soil sampling and analysis

Three soil samples were taken along one transect in each wetland: at the center of the wetland, transect midpoint, and at the edge. Soil samples were collected with a soil

probe to a depth of $\sim$15 cm. Upon return from the field, soil samples were oven dried and then passed through a 2 mm sieve and stored for analysis.

Soil organic matter was measured as loss-on-ignition using 0.5 kg of soil ashed at 450°C for 16 h. Ash was analyzed for total P (Allen et al. 1974) by extracting with aqua regia (Murphy and Riley 1962). Phosphorus was analyzed for soil and expressed as soil total P (μg g^{-1}). Soil pH was measured in a slurry (5 g soil, 25 ml distilled water) using an Orion pH meter (model 230A). The slurry was shaken and then allowed to incubate for 30 min before measuring pH. A microplate spectrophotometer (μQuant Microplate Spectrophotometer, BioTek Instruments, Winooski, VT) was used to analyze samples for total P using a modified malachite green method (D'Angelo et al. 2001).

Data analysis

Species data were converted to a presence–absence matrix consisting of 60 wetlands by 128 species. We used Nonmetric Multidimensional Scaling (NMS; PC-ORD v. 4) to compare vegetation composition among pasture-types. The effect of pasture, total P, soil pH, wetland size, isolation, and mean CC/wetland were compared with a joint plot and correlations with axis scores. NMS is suitable for heterogeneous data sets with many shared zeros among sampling units (wetlands in our case) and does not assume linear relationships among variables (McCune and Grace 2002). For these analyses, we used Sørenson distance, a city block distance measure expressed as a proportion of the maximum distance. This distance measure was selected because it fits heterogeneous vegetation patterns better than other commonly used distance measures such as Euclidean distance (McCune and Grace 2002). Coefficient of variation among wetlands and species were 35.9 and 128.4% respectively; no transformations of the matrix were necessary. We selected a three dimensional solution based on the lowest stress. A randomization test of the final stress based on 500 iterations showed significant structure in the data (p = 0.02). This solution explained 83% of the variation in the data set ($r^2 = 0.33$, 0.17, and 0.33 for axis 1, 2, and 3 respectively). Multi-response permutation procedures (MRPP) were used to determine if vegetation composition differed between the two pasture-types (McCune and Grace 2002). Before testing hypotheses, we determined collinearity among variables (Table 1). Wetland area was log transformed to reach normality for analyses.

To better evaluate community composition, we used both native and exotic species richness as dependent variables in ANCOVAs to assess the effect of pasture-type, total P, soil pH, wetland size and isolation on vegetation. In this analysis, pasture-type was used as a fixed effect and total P, soil pH, wetland size and isolation were used as covariates. Coefficient of conservatism (CC) scores were not used in this analysis because it was a less straightforward test of the idea that pasture intensification would favor niche assembly versus dispersal assembly. For example, if the importance of wetland isolation to species richness varies with pasture-type, it is likely that this effect may be related to the importance of dispersal. However, since mean CC scores are independent of species richness, it is less clear how isolation should affect mean CC in managed landscapes. We used a general linear model assuming the Poisson distribution (appropriate for count data). We tested 30 possible models, iteratively fitting models starting with the full factorial model and systematically assessing models with all four-way, three-way, and two-way interactions, a main effects model and then single main effects of each of the five covariates (pasture, pH, total P, wetland isolation, and wetland size). From 120 different possible model combinations with these five covariates, we narrowed our model selection to 30 of them to specifically examine the pasture:isolation interaction (Burnham and Anderson 2002). To identify the most useful model based on explanatory power and likelihood we used Akaike information criterion (AIC). We chose the lowest AIC score and highest model weight as the most parsimonious model. We calculated model AIC weights which indicate the likelihood of the model in comparison to other considered models. All univariate statistical analyses were performed via R software (v 2.6.1; R Development Core Team 2007).

Results

Soil total phosphorus and plant assemblages differed between wetlands in improved pastures and in semi-native pastures. Wetlands in intensely managed improved pasture had higher soil total P than did wetlands in semi-native pasture wetlands (Table 2). Improved pasture wetlands also had lower species richness (one-way ANOVA, $F_{(1,58)} = 4.87$, p = 0.031; Table 2) and CC scores (one-way ANOVA, $F_{(1,58)} = 24.484$, p < 0.0001; Table 2) and greater percent cover of exotic species than in less intensively managed semi-native pasture wetlands (Table 2). Semi-native pasture wetlands had lower soil P levels, higher CC scores and greater native species richness and were dominated by grasses (*Panicum* spp.), sedges

Table 1. Correlation matrix of the independent variables used in ANCOVA.

	Size	Isolation	pH	Total P
Size	1.0	–	–	–
Isolation	0.39	1.0	–	–
pH	0.19	0.28	1.0	–
Total P	−0.34	−0.44	−0.44	1.0

Table 2. Characteristics of wetlands by surrounding upland pasture-type (mean ± standard deviation). The *symbol indicates that the differences in the values are significant, one-way ANOVA, p ≤ 0.05.

	Improved pasture wetlands	Semi-native pasture wetlands
Sample size	30	30
Area (ha)	1.41 ± 3.15	0.93 ± 1.93
Species richness*	20.67 ± 1.22	24.37 ± 1.65
Exotic cover (%)*	7.62 ± 5.26	0.69 ± 0.98
Mean CC*	2.46 ± 0.51	3.12 ± 0.52
Soil total P (μg g^{-1})*	264.14 ± 122.83	195.75 ± 77.00
Soil pH	4.52 ± 0.57	4.51 ± 0.36

(*Rhynchospora* spp.), and emergent vegetation such as *Pontederia cordata* L. and *Sagittaria lancifolia*.

The NMS ordination indicated two distinct plant communities defined by pasture-type (Fig. 3). MRPP revealed these groups were statistically different (p < 0.0001). Axis 1 of the ordination was associated with a gradient in total phosphorus that increased towards the area of improved pasture wetlands. Axis 2 was associated with pH, though pH was not clearly related to pasture-type. Wetland area was weakly associated with axis 3 and isolation was weakly associated with both axis 1 and 2 (Table 3). Axis 1 was significantly positively associated to wetland mean coefficient of conservatism scores (Table 3); with mean CC scores increasing towards the semi-native pasture wetland cluster (Fig. 4). Axis 3 was significantly positively related to native species richness (Table 3). These results support the idea that increased soil P may reduce floristic quality in wetlands.

The model with the lowest AIC of native species richness included the main effects of wetland size, isolation, total P,

Table 3. Pearson correlations (r) between variables and ordination axes. The *symbol indicates significance at the 0.05 level and **at the 0.01 level.

	Axis 1	Axis 2	Axis 3
ln(size)	0.09	0.26*	0.34**
ln(isolation)	0.37**	0.38**	0.27*
pH	0.10	0.56**	−0.26*
Total P	−0.52**	−0.33*	0.02
Native species richness	0.32*	0.27	0.53**
Mean CC score/wetland	0.78**	−0.04	0.30*

and pasture as well as various two and three-way interactions (Table 4 and 5). In this model, the coefficient for the main effect of wetland size was significant, with diversity increasing with area (Table 5). Pasture-type was also significant, with higher richness in the semi-native pasture wetlands (Table 5). We found a significant interaction of wetland size and pasture-type caused by a strong species–area relationship in improved pasture wetlands, but not in semi-native pasture wetlands (Fig. 5). There was a highly significant interaction between pasture-type and isolation reflecting a strong relationship of degree of wetland isolation with native species richness in semi-native and absence of such relationship in improved pasture wetlands (Fig. 6a), supporting our hypothesis that land-use intensity decouples the relationship between isolation and species richness. The significant three-way interactions (Table 5) indicated that the relationship between total P, size, and isolation contributed to variation in native richness. Smaller and more isolated wetlands had greater total P levels (Fig. 7a, b). The model with the lowest AIC predicting exotic species richness included only the main effect of wetland isolation, where exotic richness decreased with greater wetland isolation in both pasture-types (z = 2.28, p = 0.02; Fig. 6b).

Discussion

Pasture intensification affected wetland vegetation by promoting exotic and/or invasive species and decreasing
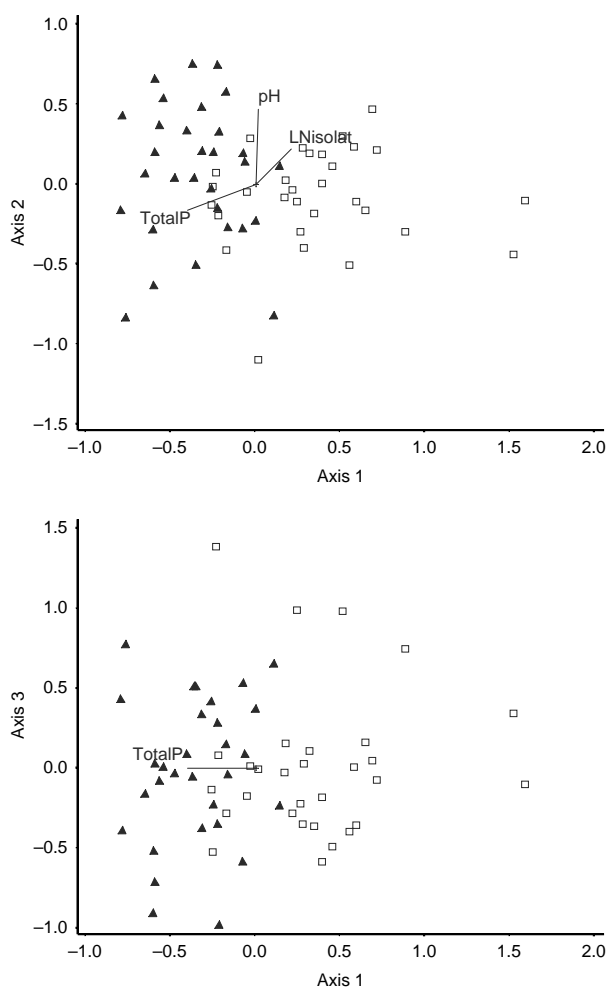

Figure 3. NMS ordination of wetlands in plant species space with joint plot of wetland size, isolation, pH, and total P. Radiating lines indicate the strength and direction of correlations between individual variables and the strongest gradients in species composition. Each symbol represents one wetland. Black triangles represent improved pasture wetlands and white squares represent semi-native pasture wetlands.
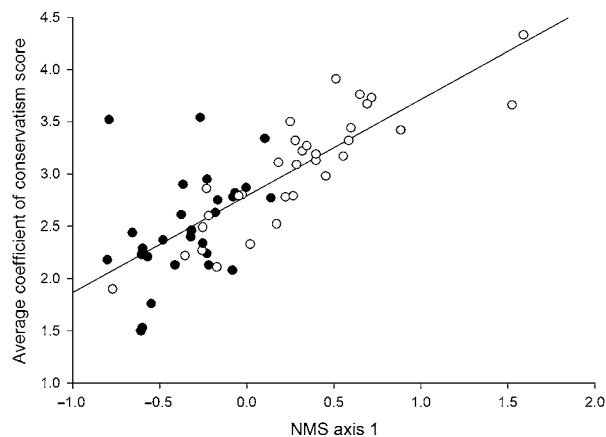

Figure 4. NMS axis 1 is significantly related to mean coefficient of conservatism scores ($r^2 = 0.61$). Each symbol represents one wetland. Black circles represent improved pasture wetlands and white circles represent semi-native pasture wetlands.

Table 4. ANOVA table of significance of coefficients in the best model predicting native species richness.

	Coefficient	SE	DF	z	p
ln(size) (S)	0.40	0.26	1	2.59	**0.009**
ln(isolation) (I)	−0.19	0.13	1	−1.41	0.16
Total P (T)	−0.002	0.0009	1	−1.66	0.09
Pasture (P)	−1.75	0.57	1	−3.08	**0.002**
S:I	−0.11	0.08	1	−1.43	0.15
S:P	−0.48	0.19	1	−2.55	**0.01**
I:P	0.70	0.20	1	3.46	**0.0005**
S:T	−0.0008	0.0004	1	−1.73	0.08
I:T	0.0008	0.0005	1	1.69	0.09
T:P	0.007	0.003	1	2.50	**0.01**
S:I:T	0.0003	0.0002	1	1.22	0.22
S:T:P	0.002	0.0007	1	2.07	**0.04**
I:T:P	−0.003	0.0009	1	−2.66	**0.008**

native species richness. Many species native to Florida developed in low soil P environments and are replaced by weedier, more generalist species when P levels increase (Qualls and Richardson 1995, Gathumbi et al. 2005, Tweel and Bohlen 2008). In particular, native *Juncus effusus* var. *solutus* becomes dominant in improved pasture wetlands, in turn affecting vegetation structure and distribution of organic matter and soil nutrients (Gathumbi et al. 2005, Tweel and Bohlen 2008). *Juncus effusus* is unpalatable to cattle and increases with grazing pressure possibly due to release from competition by selective grazing (Tweel and Bohlen 2008).

Our finding that native species richness increased with wetland size is in agreement with other observations of a species-area relationship in wetland plants (Møller and Rørdam 1985, Matthews et al. 2005). However, the species-isolation relationship in wetland plants has been less clear. We found that isolation effects were most apparent when more sophisticated measures of isolation were used and when distances were calculated between wetland edges rather than between wetland centroids (Fig. 2). Distances between wetland centroids are farther than distances between wetland edges and do not realistically portray the amount of terrestrial habitat wetland plant propagules must traverse, especially because many wetland plants occupy wetland edges rather than deeper centers. Other commonly-used isolation measures (i.e. distance to the nearest wetland or average distance between the nearest three wetlands) were relatively poor measures of isolation. Importantly, our analysis suggests that source wetland area may be more important to dispersal compared to distance between wetlands (Fig. 2). The fact that semi-native pastures contained larger wetlands than improved pastures (Fig. 1) may explain why the isolation index was more strongly related to species richness than in improved pasture wetlands. The reduction of wetland area in more intensely managed land-uses may be one of the key factors that negatively affect species richness and may be a historical aspect relating to pasture conversion activities.

Our analyses emphasized the importance of spatial scale on the relationship between species richness and isolation (Fig. 2). We found that isolation had the greatest impact on species richness within radii of 400–700 m in semi-native pastures, roughly comparable to results in Swedish grasslands (Lindborg and Eriksson 2004, Cousins 2006, Cousins et al. 2007). Semi-native pastures are similar to native prairie habitat (Orzell and Bridges 2006), and thus the results of our study may be generalized to other seasonal wetlands embedded in prairies if species have similar dispersal abilities as those in our study.

Native species richness was affected by wetland isolation in semi-native pasture wetlands but weakly related to

Table 5. Top five models and the main effects model from AIC model comparisons. Log(£) =maximized log-likelihood, K =no. of parameters, AIC =Akaike information criterion value, Δ_i =difference between the lowest AIC value and AIC_i, w_i =model weight given the data. (:) denotes an interaction term. S: ln(size); I: ln(isolation); T: total phosphorus; P: pasture; pH: pH.

| Model	Log(£)	K	AIC	Δ_i	w_I
Native species richness					
S+I+T+P+S:I+S:P+I:P+S:T+I:T+T:P+S:I:T+S:T:P+I:T:P	−179.3	14	**386.7**	0	**0.62**
S+I+T+P+S:I+S:T+S:P+I:T+I:P+T:P+S:I:T+S:T:P+I:T:P+S:I:T:P	−178.8	16	389.5	2.9	0.15
S+I+T+pH+S:I+S:T+S:pH+I:T+I:pH+T:pH+S:I:T+S:T:pH+I:T:pH+S:I:T:pH	−179.1	16	390.3	3.6	0.10
S+I+P+S:I+S:P+I:P+S:I:P	−187.2	8	390.4	3.7	0.09
S+I+T+S:I+S:T+I:T+S:I:T	−188.3	8	392.6	5.9	0.03
S+I+T+P+pH	−205.2	6	422.4	35.7	1.1×10^{-8}
Exotic species richness					
I	−107.86	2	**219.7**	0	**0.38**
I+P+I:P	−107.19	4	222.4	2.7	0.10
P	−109.20	2	222.4	2.7	0.09
I+T+I:T	−107.23	4	222.5	2.7	0.09
I+S+I:S	−107.50	4	223.0	3.3	0.07
S+I+T+P+pH	−107.43	6	226.9	7.1	0.01
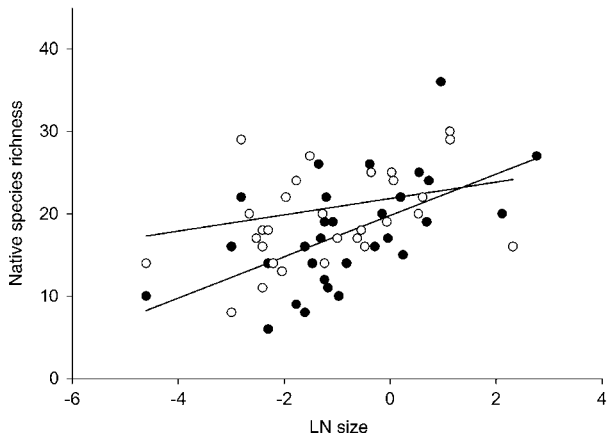
Figure 5. Native species richness is significantly positively related to wetland size in improved pasture wetlands (black), but not in semi-native pasture wetlands (white).

wetland isolation in improved wetlands. Additionally, the species-area relationship was stronger in improved wetlands than semi-native wetlands. Taken together, these results suggest that community assembly reflected persistent dispersal-based assembly processes in semi-native wetland vegetation (Fukami et al. 2005), but was strongly influenced by environmental conditions (fertilization, grazing, and soil disturbance) favoring tolerant species in improved wetland vegetation. This result suggests that the strength of
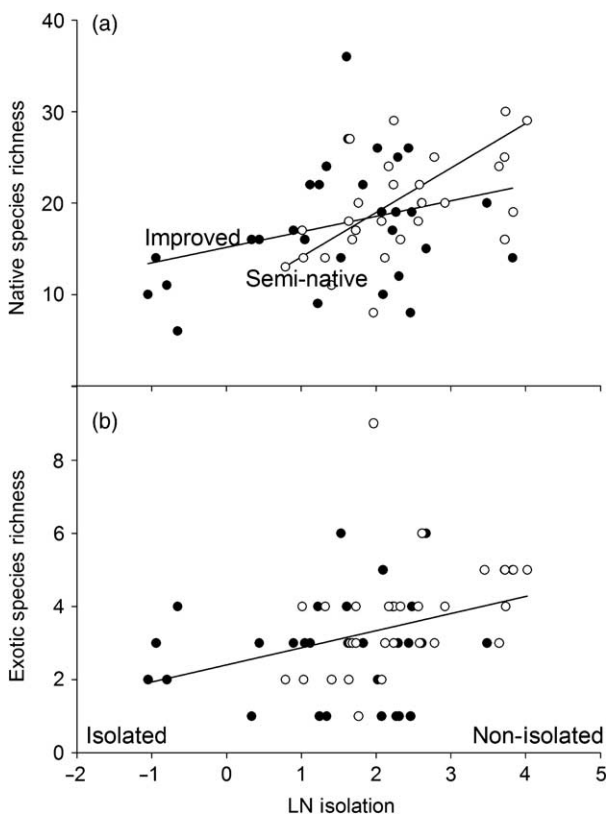
Figure 6. (a) Native species richness is significantly related to isolation in semi-native pasture wetlands (white), but not in improved pasture wetlands (black). (b) Exotic species richness is related to isolation in both pasture-types.

isolation effects and residual variance in a species–area curve may indicate the relative strengths of dispersal- and niche-based processes in metacommunity assembly (Chase and Liebold 2003).

Although pasture intensification influenced how native species assemblages responded to wetland isolation, it did not influence the effect of isolation on exotic species richness. Exotic species richness decreased with increasing wetland isolation in both pasture types suggesting some ongoing dispersal limitation (i.e. ongoing colonization) for exotics. Since exotic species are more likely to tolerate disturbance (such as increased cattle activity) and are often good competitors, pasture-intensification does not prevent them from becoming established in improved pastures wetlands as it does for some native species.

A caveat to this study is that historical data are not available for these wetlands, so we cannot evaluate whether there were differences between wetlands in these pasture types prior to conversion to pastures. Though slight topographical differences between pasture types (1–3 m elevation) may have influenced community assembly mechanisms prior to conversion, wetlands in such close proximity (Fig. 1) with similar hydroperiods (∼6 months) were probably governed by comparable processes with similar diversity (Kushlan 1990). However, it still remains to be tested whether dispersal limitation could also possibly be controlled by topography (in addition to spatial isolation) as these wetlands are periodically hydrologically connected due to flooding.

In summary, more intensive land-use in pastures, which included a combination of greater stocking rates, conversion of upland pasture and increased soil phosphorus, was associated with declines in native plant species richness and coefficient of conservatism scores. Isolation affected native plant composition in wetlands embedded within semi-native pastures, but the disturbed conditions in wetlands embedded within intensively-managed pastures had a greater impact than isolation on native species richness. Exotic species richness was affected only by wetland isolation, suggesting exotic colonization of wetlands continues. Our results indicate that a) native species switch from dispersal-based community assembly in semi-native pastures to a species-sorting process in the environmentally-stringent "improved" pastures, and b) recently-introduced exotic species already sorted for ranch conditions are primarily undergoing dispersal-based community assembly. That land-use may alter the relative importance of assembly processes and that different processes drive native and exotic richness has implications for both ecosystem management and restoration planning. If composition is driven by species' tolerances in disturbed environments, managers could focus more on altering environmental conditions, such as lowering nutrients or providing sufficient landscape buffers around wetlands with conservation priority. However, if communities are dispersal-assembled, active restoration techniques such as seed additions may be required. Our finding that exotics are dispersal limited suggests that non-native species control should focus on factors that facilitate dispersal of these species.
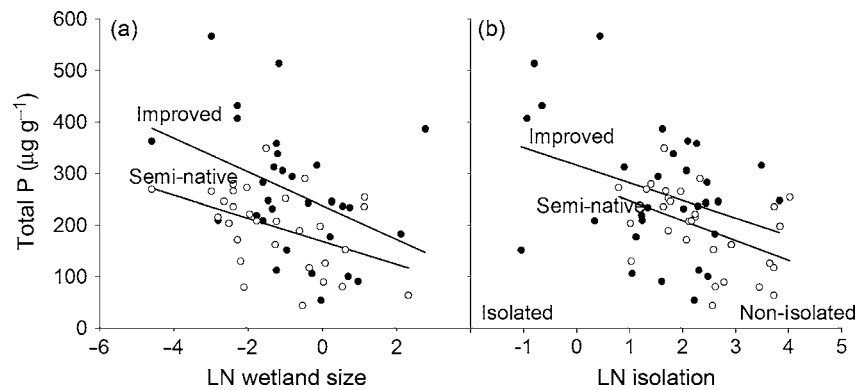
Figure 7. (a) Total P declines with increasing wetland size in both pasture-types (improved wetlands = black, semi-native wetlands = white). (b) Total phosphorus declines as wetland isolation declines.

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