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# Testing wetland features to increase amphibian reproductive success and species richness for mitigation and restoration

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**Abstract.** Aquatic habitat features can directly influence the abundance, species richness, and quality of juvenile amphibians recruited into adult populations. We examined the influences of within-wetland slope, vegetation, and stocked mosquito fish (*Gambusia affinis*) on amphibian metamorph production and species richness during the first two years post-construction at 18 experimental wetlands in northeast Missouri (USA) grasslands. We used an information theoretic approach (AIC<sub>c</sub>) to rank regression models representing total amphibian metamorph production, individual amphibian species metamorph production, and larval amphibian species richness. Total amphibian metamorph production was greatest at shallow-sloped, fish-free wetlands during the first year, but shallow-sloped wetlands with high vegetation cover were best the second year. Species richness was negatively associated with fish and positively associated with vegetation in both survey years. Leopard frog (*Rana blairi/sphenocephala* complex) metamorph quality, based on average metamorph size, was influenced by slope and the number of cohorts in the wetland. However, the tested variables had little influence on the size of American toads (*Bufo americanus*) or boreal chorus frogs (*Pseudacris maculata*). Our results indicate that wetlands designed to act as functional reproductive habitat for amphibians should incorporate shallows, high amounts of planted or naturally established vegetation cover, and should be fish-free.

**Key words:** amphibian colonization; compensatory mitigation; *Gambusia affinis*; habitat restoration; mosquito fish; wetland design.

## INTRODUCTION

Restoration ecology by its very nature is manipulative and can provide valuable opportunities to test the effectiveness of various ecological factors in restoring regional biodiversity (Young 2000, Young et al. 2005). Restoration or compensatory mitigation often resets successional processes, restarts disturbance regimes, and can favor invasive species proliferation, especially in aquatic ecosystems (Zedler 2000, Young et al. 2001). Predicting ecological succession is challenging in all restoration projects, but particularly in the case of wetland restorations where regulatory constraints call for specific outcomes on small sites in relatively short time periods (Zedler 2000). While establishing a minimum hydroperiod and hydric vegetation can constitute “successful” wetland restoration, these criteria often overlook the importance of ensuring habitat and species diversities. Once wetland construction is complete, it is often assumed that wildlife will colonize and use the habitat as they would natural wetlands. The presence of habitat generalists may reinforce this “build

it and they will come” philosophy, and their presence can conceal the shortcomings of restoration efforts for habitat specialists that may suffer the most from natural wetland losses.

Constructed wetlands are generally devoid of substrate topographic and hydroperiod diversity. As a result, open water may lack more desirable natural wetland characteristics (National Research Council 2001, Porej 2003, Shulse et al. 2010). Aquatic vegetation structure, substrate topography, predation risk, and hydroperiod are critical factors influencing the community composition and reproductive success of wetland fauna (Pechmann et al. 1989, 2001, Semlitsch et al. 1996, Brooks 2000, Fairbairn and Dinsmore 2001, Porej and Hetherington 2005, Indermaur et al. 2010). As several studies have indicated, aquatic breeding amphibians benefit from vegetated littoral zones that provide refuge from predators, areas for foraging and thermoregulation, substrates for oviposition, and calling sites for male anurans (Stratman 2000, Semlitsch 2002, Hazell et al. 2004, Hartel et al. 2007). The effects of fish and other predators are also mitigated by vegetation and aquatic features (Babbitt and Tanner 1997, Tarr and Babbitt 2002). However, predators small enough to penetrate dense vegetation, and those that forage in shallows frequented by larval amphibians, will likely reduce

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reproductive success. These reductions may be especially dramatic when predator density is high.

Mosquito fish (western mosquito fish [*Gambusia affinis*], eastern mosquito fish [*G. holbrooki*]) are small poeciliids native to the southern United States but introduced throughout the world for mosquito control. Mosquito fish often occur in high densities and there is growing evidence indicating that they negatively impact native ecosystems and their indigenous fauna, including amphibians (Pyke 2008). Mosquito fish reproduce rapidly, they can easily colonize new water bodies through surface water connections from release sites, and they tolerate pollution and low dissolved oxygen (Lawler et al. 1999). Although they forage in shallows and can penetrate dense vegetation, it is unclear if these habits increase their exposure to larval amphibians or if vegetation attenuates predation risk (Webb and Joss 1997, Lawler et al. 1999).

Amphibians exhibit interspecific differences in their sensitivity to environmental degradation and are therefore important indicators of the quality of aquatic communities and their associated terrestrial environments (Micacchion 2004). Nevertheless, managers and researchers often overlook them when designing or monitoring restored or newly constructed wetlands (National Research Council 2001, Porej and Hetherington 2005). Amphibians provide a significant biological nexus between wetland and upland habitats because they transfer large amounts of energy, nutrients, and biomass between the two ecosystems (Gibbons et al. 2006, Semlitsch and Skelly 2007). The fact that most species require suitable aquatic and terrestrial habitats to complete their life cycles poses special challenges for both the design and placement of wetlands in the landscape (Pellet et al. 2004, Shulse et al. 2010). Both aquatic and nearby landscape features are necessary to consider during wetland planning. An appropriately designed aquatic habitat will directly influence the species, number, and quality of metamorphosing juveniles recruited into terrestrial adult populations (Semlitsch 2002), and the persistence of species within wetland ecosystems (Hamer and Parris 2011).

Building on common wetland restoration and mitigation practices, we examine the assembly of amphibian communities in experimental wetlands constructed de novo, as can often be the case in wetland restoration and mitigation. Although a number of studies have revealed correlations between amphibian populations and the presence or abundance of fish, vegetation cover, or slope (i.e., Knutson et al. 2004, Porej and Hetherington 2005, Shulse et al. 2010), none have explicitly tested these features. Our objective was to investigate the influence of these features on amphibian populations at replicate constructed wetlands. We hypothesized that planting vegetation and creating shallow within-wetland slopes would increase metamorph production and species richness, while mosquito fish would reduce both measures.

## METHODS

### *Study areas and design*

During October and November 2006, we constructed six wetlands at each of three Missouri Department of Conservation (MDC) upland grassland habitats in northeastern Missouri (USA) ( $n = 18$  wetlands; Fig. 1). Distances between the three habitats were 15 km (White and Sears), 71 km (White and Redman), and 85 km (Sears and Redman). This region of Missouri has 16 species of pond-breeding amphibians (Daniel and Edmond 2010). Each grassland area had forest nearby, but in varied amounts. We attempted to place wetlands at roughly equal distances from forest cover within each study site to control dispersal distance from potential source populations. We also attempted to place wetlands at roughly equal distances from each other within study sites, but distances varied due to placement limitations (63–242 m, mean 117.5 m). We randomly assigned one of the six treatment combinations of littoral zone slope (steep 4:1 vs. shallow 15:1), mosquito fish (*Gambusia affinis*, stocked vs. unstocked), and vegetation (planted vs. unplanted; Table 1) to each wetland. Each wetland was round, 23 m diameter, and 0.76 m maximum depth. Shallow-sloped wetlands came to a point at the center where maximum depth was reached. Steep-sloped wetlands had 16 m diameter circular bottoms at maximum depth (Appendix A: Fig. A1). Wetlands were constructed using heavy equipment and a laser level was used to verify depth, slope, and size.

We chose to use 15:1 for the shallow-sloped design based on the definition of “shallows” in Porej and Hetherington (2005). The authors of that study state that the Ohio Environmental Protection Agency incorporated this ratio into replacement wetland designs. The authors also encouraged other regulatory agencies to do the same to avoid negative impacts on amphibians (Porej and Hetherington 2005). We chose 4:1 as the steep-sloped design because these are the steepest bank slopes incorporated into mitigation wetlands constructed by the Missouri Department of Transportation (MoDOT; B. Brooks, *personal communication*). Furthermore, many open-water agricultural or wildlife ponds in northern Missouri are constructed with bank slopes of 4.5:1 or steeper (Deal et al. 1997, Perry 2006, Shulse et al. 2010).

We stocked mosquito fish because they have been implicated in amphibian population declines in California, Australia, and China (Lawler et al. 1999, Pyke and White 2000, Karraker et al. 2010). Although native to southeastern Missouri, *G. affinis* has been expanding in distribution into northern Missouri through natural dispersal and undocumented introductions (Pflieger 1997). In a recent study involving surveys of constructed wetlands in northern Missouri, mosquito fish were captured in 20% of all wetlands surveyed (Shulse et al. 2010) and 45% of compensatory mitigation wetlands (C. D. Shulse and R. D. Semlitsch, *unpublished data*).

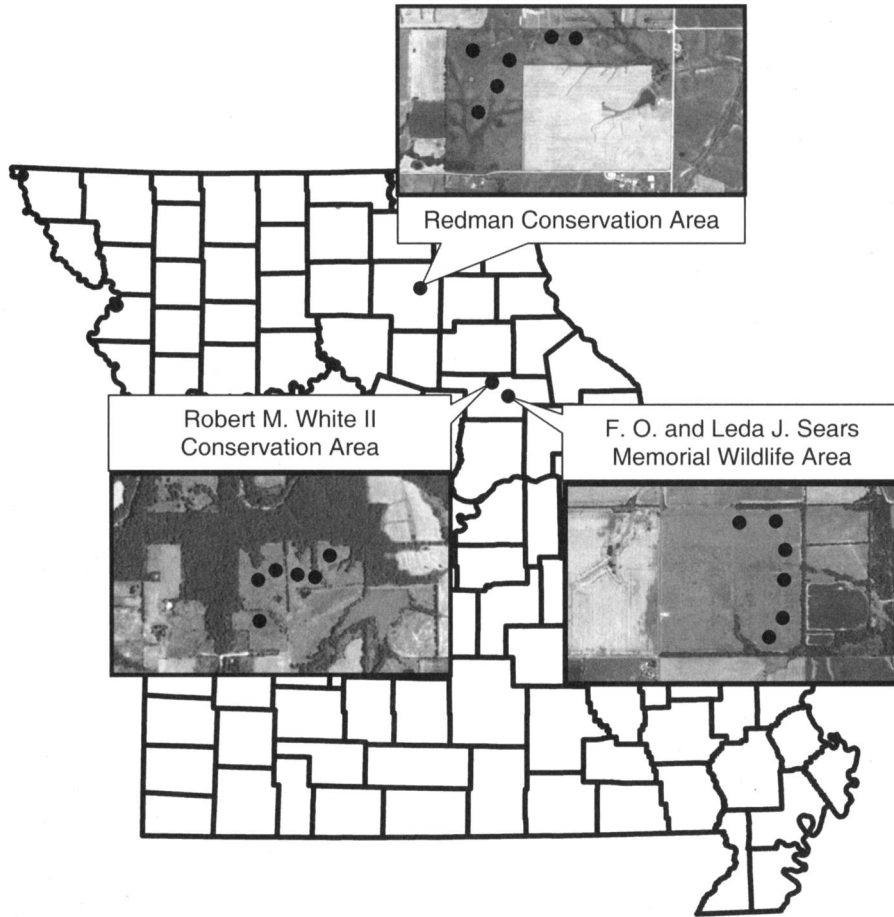


FIG. 1. Experimental wetland locations in Missouri, USA. Aerial photograph blowups illustrate the location of the six wetlands constructed at each location (black dots, not to scale), and the surrounding landscape.

MoDOT purposely introduced mosquito fish into one mitigation wetland for mosquito control in 2003 (B. Brooks, *personal communication*). We obtained mosquito fish from this wetland and introduced them within the randomly assigned experimental wetlands at a rate of 3089 fish/ha, which is slightly higher than the rate of 2471 fish/ha (1000 fish/acre) recommended by Duryea et al. (1996). This rate resulted in a founding population of 125 adult mosquito fish per stocked wetland in March 2007. Fish were restocked into wetlands where samples indicated low populations during early spring 2008. Some wetlands stocked with mosquito fish were treated with the piscicide rotenone after the current study was complete to conduct further investigations of *Gambusia* effects on aquatic communities (see Shulse 2011). Mosquito fish were removed from all stocked wetlands by MDC personnel after the study was complete.

Native prairie cordgrass (*Spartina pectinata*) plants were added in November 2006 to the wetlands receiving vegetation treatments. Cordgrass is routinely used to revegetate new compensatory mitigation wetlands constructed by MoDOT (B. Brooks, *personal communication*), and our intent was to determine if this practice

provides benefits to amphibians during early wetland development. Plants were purchased in 3.8-L pots and most were split in half prior to planting. Each wetland was planted with 50 divisions spaced apart approximately evenly and radiating from the center, and an undivided plant was placed in the center at the deepest point (Appendix A: Fig. A2). Plants that did not survive the first growing season were replaced during September and October 2007. All other vegetation was allowed to colonize and develop naturally in both planted and unplanted wetlands.

TABLE 1. Experimental wetland treatment combinations and their individual variable components.

Treatment combination	Independent variables
1	4:1 slope, fish, not planted
2	4:1 slope, no fish, not planted
3	15:1 slope, fish, not planted
4	15:1 slope, fish, planted
5	15:1 slope, no fish, not planted
6	15:1 slope, no fish, planted

### Sampling

Each wetland was completely surrounded by aluminum flashing drift fence (thin aluminum sheet) (60 cm tall) buried to depths of 10–15 cm. Paired pitfall traps were placed 5 m apart along the drift fence. Pitfall traps consisted of plastic pots (23 cm diameter  $\times$  39 cm deep) with holes drilled in the bottom for drainage and a sponge for moisture retention. Drift fence and pitfall trap arrays were installed around wetlands, after the ground had thawed, between February and late April 2007. Four gaps, each  $\sim$ 0.6–1 m wide, were incorporated into fences until all the arrays at each site were complete. The gaps were not closed, and sampling did not begin, until all arrays were complete at all sites in late April 2007. The gaps were intended to help facilitate breeding access for adult amphibians. Additionally, pitfall traps were filled with vegetation after installation to prevent captures prior to sampling. Once sampling began, the vegetation was removed and traps were generally checked every other day from May to August. Checking occurred less frequently (but at least twice per week) from mid-August to mid-September. In 2007, traps were checked from 23 April to 16 September and, in 2008, from 12 May to 9 September. Adults captured in outside traps were released inside the drift fences to facilitate breeding access to the wetlands. Juveniles captured in outside traps were excluded and released outside of fences, assuming they were dispersing from other wetlands. Excluding juveniles allowed us to reduce the chances of falsely attributing juvenile captures inside fences to production at the capture wetlands when these individuals were actually produced elsewhere. All animals captured inside the fences were released outside after recording species, snout–vent length (SVL; 5–10 individuals for large cohorts), and sex (adults). Some individuals were captured by hand inside fences and released outside after recording.

Mosquito fish were sampled three times each season using aquatic funnel traps and dip nets. Aquatic funnel trapping occurred for 48 hours per sampling session using two kinds of commercially available minnow traps: collapsible nylon mesh traps (38  $\times$  26  $\times$  26 cm; 3-mm mesh, 6-cm openings) or galvanized steel wire traps (42 cm long; 6-mm mesh, 2.5-cm openings). Two traps of each kind were used per wetland, and they were staggered so that traps of each kind were directly across from one another at each cardinal direction. Assignment of pair direction was randomly chosen. One dip net (3-mm nylon mesh) sweep ( $\sim$ 1.5 m long) was conducted from the water's edge at each cardinal direction with the net pressed to the substrate and pulled toward the sampler. During the second sampling period in 2007, a canvas D-net with 500-micron mesh bottom was added to the sampling protocol to capture macroinvertebrates and zooplankton (see Shulse 2011). Approximately 1.5-m sweeps occurred at each ordinal direction using the canvas net. This resulted in four dip net sweeps and four canvas net sweeps spaced evenly apart for each wetland

during each sampling period. Cumulative data from all aquatic sampling methods were summed to calculate mosquito fish abundance and amphibian species richness. Larval and metamorph amphibians captured during aquatic habitat sampling were included in species richness analyses even if no metamorphs of a particular species were captured in pitfall traps. Including these species in richness calculations is justified because we may have missed species during terrestrial sampling, given that some species readily escape pitfall traps and drift fences (i.e., gray tree frogs and cricket frogs), or have larval periods spanning multiple seasons (bullfrogs and green frogs). However, some species detected during aquatic sampling may have failed to successfully metamorphose and exit the wetlands for various reasons. In the latter situation, one might argue, the wetland failed to function for these species. Nevertheless, without absolute knowledge that no larvae of a particular species successfully metamorphosed from a given wetland, we believe it is not justifiable to exclude from richness calculations species that are only detected during aquatic sampling. Richness models can be interpreted as providing insight into the wetland conditions that induce breeding, oviposition, and larval growth to the size of capture; whereas the metamorph abundance models illustrate the influence of wetland conditions on reproductive success. Individuals captured during aquatic sampling were not used in metamorph production analyses.

We measured within-wetland vegetation cover using four 1-m<sup>2</sup> quadrats spaced at cardinal directions around the wetland perimeter. Quadrats were placed at the edge of the wetland to assess vegetation cover within 1 m of the shore and at 3 m from the shore. The percentages of open water, emergent, floating, and submerged vegetation were visually estimated within each quadrat. The three vegetation categories were combined and averaged for all quadrats over all sampling periods at each wetland to calculate an average measure of vegetation cover for each year. Percentage of vegetation cover was transformed to the arcsine square-root of the proportion for analyses.

### Data analysis

All statistical analyses were performed using SPSS version 16.0 (SPSS 2007). To explain the relationships between total amphibian production (reproductive success of all amphibian species) or individual species production (reproductive success of individual species) and the independent wetland design variables, we developed regression models with a negative binomial error distribution and log link function using the generalized linear model option in SPSS. To explain species richness relationships, we developed regression models with a normal error distribution and log link (2007) or identity link (2008) function. We combined data obtained from captures of southern leopard frog (*Rana sphenoccephala*) and plains leopard frog (*R. blairi*)

because some metamorphs could not be identified definitively. Similarly, we were unable to distinguish between eastern gray tree frogs (*Hyla versicolor*) and Cope's gray tree frogs (*Hyla chrysocelis*). Each model set contained combinations of all three independent variables (global: fish, vegetation, slope), two-variable models, single-variable models, and an intercept-only model. All models also included the intercept. We used mosquito fish abundance from aquatic sampling data instead of fish treatment to account for differences in fish populations that may have developed between stocked wetlands. We used vegetation treatment as a categorical variable for 2007 analyses, but in the second year, natural vegetation establishment in some wetlands outpaced those that received the vegetation treatment, so we used the continuous variable vegetation cover in our 2008 analyses. Slope treatment was categorical and assumed to remain constant in both years.

We used an information theoretic approach to compare candidate regression models and avoid overfitting (Burnham and Anderson 2002). Akaike's Information Criterion values corrected for small sample size ( $AIC_c$ ) were obtained from SPSS output, and the model within each category with the smallest value was selected as most supported. The remaining models were ranked according to their differences in  $AIC_c$  from the most-supported model in the set ( $\Delta AIC_c$ ). We calculated Akaike weights ( $W$ ) and individual variable weights ( $w$ ) to make inferences among highly supported candidates and to assess the relative importance of each variable within the entire model set (Burnham and Anderson 2002). We also calculated the percentage of deviance explained for each model by dividing the reduction in deviance for the full model by the deviance of the null model (Simon et al. 2009).

Although our primary objective was to examine the influences of the treatment variables on metamorph production and species richness, we conducted limited post hoc tests to investigate treatment influences on metamorph quality. We performed hierarchical linear regression analyses using average metamorph sizes as dependent variables. Our analyses were limited to species for which we had the largest data sets: American toads (*Bufo americanus*), boreal chorus frogs (*Pseudacris maculata*), and leopard frogs. In step 1 of the analyses, we entered the independent variables mosquito fish abundance, vegetation cover, and slope treatment. In step 2, we entered the number of metamorphs produced by the species whose average size was being used as the dependent variable. Because cohort density can influence metamorph size (Van Buskirk and Smith 1991), this procedure allowed us to control for and investigate the influences of individual species metamorph production on metamorph quality, while also examining the wetland characteristics of interest. Due to limited size data for 2007, we restricted metamorph quality investigations to 2008 data.

## RESULTS

### Metamorph production

In 2007, 13 496 metamorphs of five amphibian species were captured exiting the experimental wetlands (Appendix B: Table B1). Most (>10 700) were American toads that were produced at a single wetland that had a shallow slope, was not stocked with fish, and not planted with vegetation. Gray tree frog and boreal chorus frog metamorphs were almost exclusively captured leaving fish-free wetlands. Leopard frog metamorphs were only captured exiting shallow-sloped wetlands, and with the exception of a single individual, only captured in wetlands with planted prairie cordgrass. The only wetland treatment combination that resulted in captures of all five amphibian species detected was the shallow-sloped, no-fish, and vegetation-planted design (Fig. 2a). Over 95% of all metamorphs were produced at shallow-sloped wetlands. Excluding toads, 98% of metamorph production occurred in shallow-sloped wetlands.

Vegetation development was slow during 2007 (Fig. 3). An independent-samples *t* test was conducted to compare average annual vegetation cover for planted and nonplanted wetlands. There was a significant difference in vegetation cover between planted ( $0.22 \pm 0.02$  [mean  $\pm$  SD]) and nonplanted ( $0.03 \pm 0.05$ ;  $t_{16} = -8.47$ ,  $P \leq 0.001$  [two-tailed]).

In 2008, four times more metamorphs (56 617) and twice the number of metamorph amphibian species (10) were captured leaving the experimental wetlands (Appendix B: Table B1). Again, American toads were most abundant, with nearly 29 000 produced. Over 18 000 were again produced at a single wetland (shallow-sloped, fish-stocked, vegetation-planted; Fig. 2), but adjacent to the wetland that produced the largest numbers in 2007. American toads, boreal chorus frogs, and leopard frogs were commonly captured (detected in >10 wetlands with >1000 individuals in some wetlands). Northern cricket frogs (*Acris crepitans*) were only captured at six wetlands, and no more than three individuals were captured at a single wetland. Only two smallmouth salamanders (*Ambystoma texanum*) were captured, each from different wetlands. Gray tree frogs were captured at four wetlands with no more than three individuals captured at a single wetland. Spring peepers (*Pseudacris crucifer*) were captured at only three wetlands (two individuals per wetland). Bullfrogs (*Rana catesbeiana*) were captured in six wetlands (five at White, one at Redman) with a maximum of six individuals at a single wetland. Green frogs (*Rana clamitans*) were found at 11 wetlands, with a maximum of 14 individuals captured at a single wetland. Over 93% of metamorph production in 2008 was in shallow-sloped wetlands (89% with toads excluded).

During 2008, natural vegetation establishment in some of the nonplanted wetlands outpaced and exceeded vegetation cover in those that were planted (Fig. 3). There was no significant difference in vegetation cover

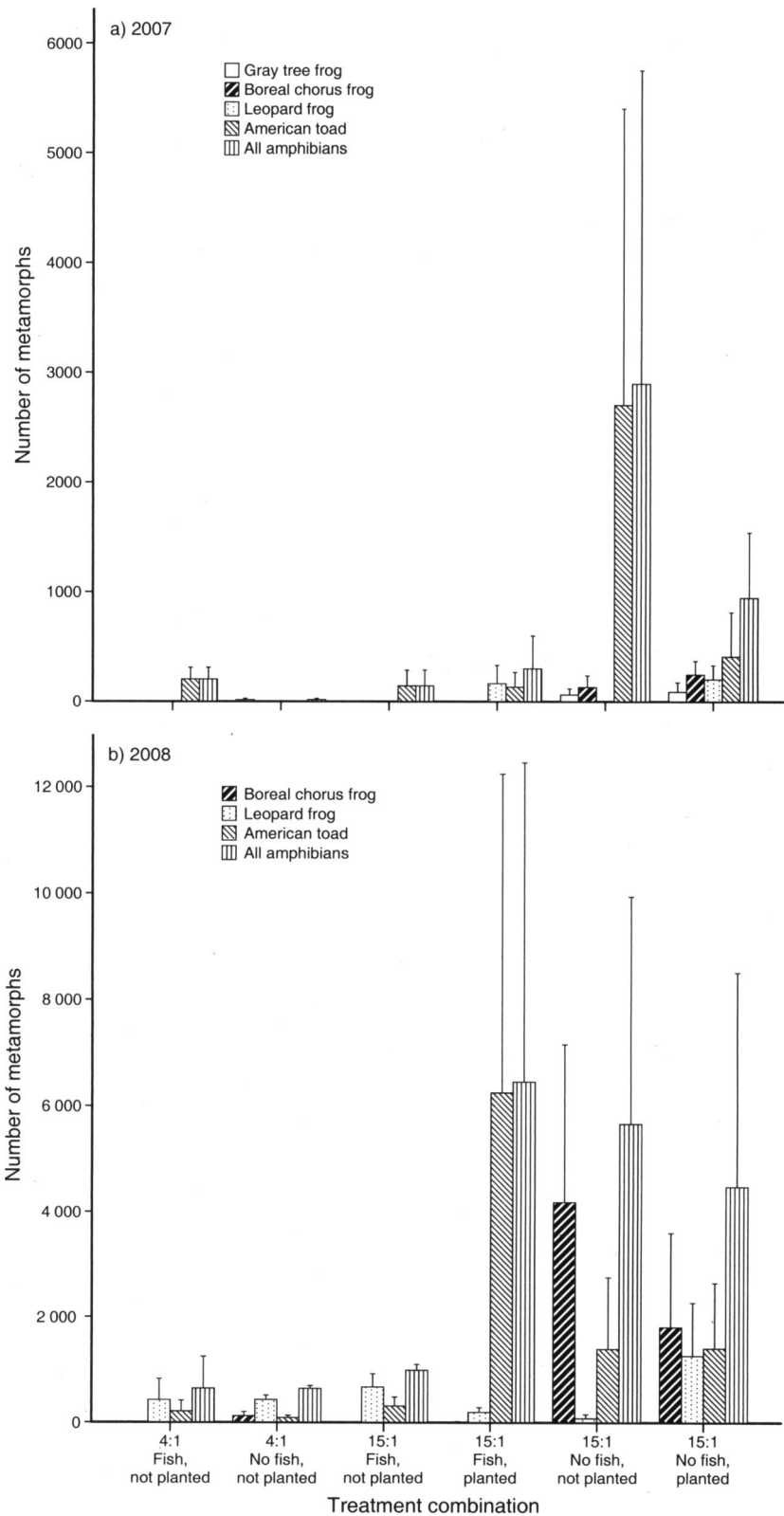


FIG. 2. Number (mean  $\pm$  SE) of metamorphs of selected amphibian species produced in (a) 2007 and (b) 2008 based upon treatment combination and slope (4:1, steep slope; 15:1, shallow slope). The ratios (4:1, 15:1) are the steep vs. shallow slope treatments, interpreted as length : depth.

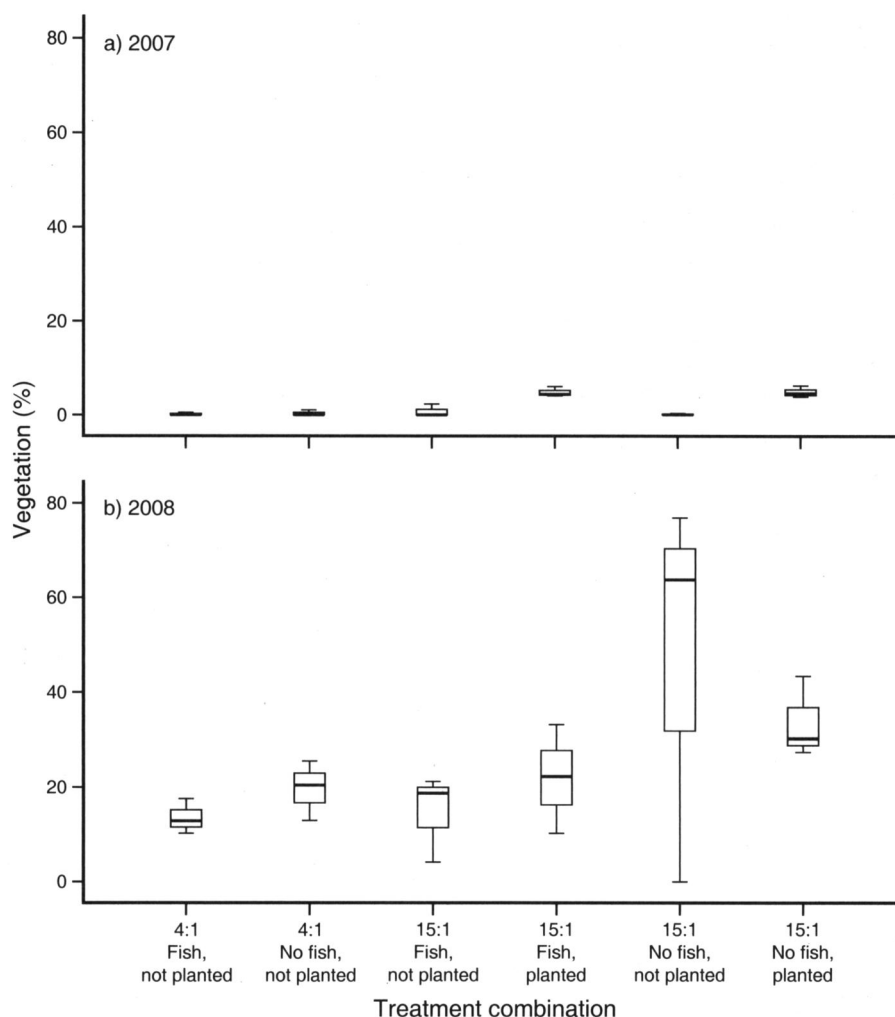


FIG. 3. Boxplots illustrating percentage vegetation cover for each wetland treatment combination and slope. The top and bottom of the boxes represent the interquartile range (50% of the cases), the line within the box is the median, and the whiskers represent the entire range.

between planted ( $0.55 \pm 0.13$ ) and nonplanted ( $0.47 \pm 0.29$ ;  $t_{16} = -0.64$ ,  $P = 0.53$  [two-tailed]) during 2008.

The global models for 2007 total metamorph production, and individual species production of toads, gray tree frogs, chorus frogs, and leopard frogs, fit the data and were significant (all  $P < 0.01$ ). In 2008, only the global models for total metamorph production and individual species production of toads, chorus frogs, and bullfrogs fit the data and were significant (all  $P < 0.05$ ). Therefore, we only conducted AIC analyses for 2008 total metamorph production and the individual metamorph productions for these three species.

Total metamorph production during the first year post-construction was best explained by a negative association with littoral zone slope (Table 2 and Appendix C: Table C1). Two additional models (FISH and FISHSLOPE) also had high empirical support ( $\Delta\text{AICs} \leq 2$ ) and total metamorph production was negatively associated with both variables. Slope also had

the highest weight as an individual variable ( $w = 0.78$ ), but the percentage of deviance explained by the SLOPE model, and the other candidate models, was rather low ( $< 16\%$ ).

During 2008, total production was best explained by the VEGSLOPE model ( $W = 0.45$ ), but the single-variable VEG model ranked almost as high ( $W = 0.35$ ,  $\Delta\text{AIC} = 0.52$ ). Total production was positively associated with vegetation cover, but as in the first year, negatively associated with slope. As an individual variable, vegetation cover was very important within the set of candidate models ( $w = 0.99$ ).

Although the percentage of deviance of the global model for American toads in 2007 was low (12.1%), their abundance was best explained by the VEGSLOPE model, and they were negatively associated with both variables. The SLOPE model also had high support ( $\Delta\text{AIC} = 1.5$ ) and was highly ranked as an individual variable ( $w = 0.77$ ). The VEGSLOPE model was again



TABLE 2. AIC<sub>c</sub> selected regression models, model and individual variable weights, and statistics for each independent variable in the selected model.

Species	Year	Model†	W‡	K§	Deviance (%)¶	Variable	w#	β	SE	Wald χ <sup>2</sup>	95% CI	
											Lower	Upper
A) Amphibians												
American toad	2007	VEG(-) + SLOPE(-)	0.39	3	11.4	slope	0.77	-14.64	4.19	12.22	-22.85	-6.43
						veg.	0.57	-1.67	0.75	4.86	-3.14	-0.18
	2008	VEG(+) + SLOPE(-)	0.32	3	23.5	veg.	0.77	5.50	2.27	5.88	1.06	9.95
						slope	0.75	-10.06	4.16	5.85	-18.21	-1.91
Gray tree frog complex	2007	FISH(-)	0.43	2	51.2	fish	0.99	-0.06	0.01	19.26	-0.09	-0.04
Leopard frog complex	2007	VEG(+)	0.79	2	73.0	veg.	1.00	7.70	1.12	47.39	5.51	9.89
Boreal chorus frog	2007	FISH(-) + SLOPE (-)	0.78	3	71.3	fish	0.99	-0.06	0.01	50.07	-0.08	-0.04
						slope	0.99	-27.53	4.68	34.66	-36.69	-18.36
	2008	FISH(-) + VEG(+)	0.69	3	60.3	fish	0.99	-0.04	0.01	36.77	-0.06	-0.03
						veg.	0.97	8.04	2.22	13.05	3.68	12.40
Bullfrog	2008	VEG(-)	0.38	2	17.3	veg.	0.87	-3.26	1.45	5.07	-6.10	-0.42
B) Combined values												
Total production	2007	SLOPE(-)	0.45	2	12.0	slope	0.78	-12.66	3.41	13.80	-19.35	-5.98
						veg.	0.99	4.80	1.46	10.74	1.93	7.67
	2008	VEG(+) + SLOPE(-)	0.45	3	40.7	slope	0.55	-5.67	2.90	3.82	-11.35	0.01
Species richness	2007	FISH(-) + VEG(+)	0.67	3	46.0	veg.	0.95	-0.01	0.004	5.66	-0.02	-0.002
						fish	0.92	0.88	0.27	10.85	0.34	1.40
	2008	FISH(-) + VEG(+)	0.42	3	31.9	fish	0.83	-0.01	0.003	5.31	-0.01	-0.001
						veg.	0.66	2.04	1.04	3.87	0.01	4.07

Note: Full AIC<sub>c</sub> analysis results are given in Appendix C: Table C1.

† VEG represents vegetation treatment in 2007 models and vegetation cover in 2008 models.

‡ Akaike weight can be interpreted as the probability that the model is the best-approximating model in the set.

§ Number of estimable parameters in the model, including the intercept.

¶ Percentage deviance is the reduction in deviance for the model divided by the deviance of the null (intercept-only) model.

# Individual variable weights can be interpreted as the relative importance of that variable in the model set.

|| Leopard frog global model contained only the variables vegetation treatment and mosquito fish abundance.

ranked highest in 2008. However, toads were positively associated with vegetation cover during the second year. Several models had high empirical support within the set, but all contained a positive association with vegetation cover and/or a negative association with slope. As individual variables, both vegetation cover and slope ranked highly ( $w = 0.77$  and  $0.75$ , respectively).

Gray tree frogs were negatively associated with mosquito fish in 2007. The FISH model best explained their abundance and it was very highly ranked as an individual variable ( $w = 0.99$ ). In 2008, gray tree frogs were not captured in wetlands containing fish, so the global model contained only vegetation cover and slope. The global model did not fit the data ( $\chi^2 = 0.25$ ,  $df = 2$ ,  $P = 0.88$ ) so no further analyses were conducted.

Because leopard frog metamorphs were only captured leaving shallow-sloped wetlands during 2007, only the variables fish abundance and vegetation treatment were included in the 2007 global model for these amphibians. The best model explaining leopard frog abundance was VEG. Leopard frogs were positively associated with the planted cordgrass, and we found only one metamorph exiting a wetland that was not planted. Our results are reflected in the individual variable weight of 1 for vegetation. In 2008, leopard frog metamorphs were nearly ubiquitous and were captured exiting almost all wetlands. All three independent variables were included

in the leopard frog global model, but the model did not fit the data ( $\chi^2 = 2.1$ ,  $df = 3$ ,  $P = 0.55$ ).

The FISHSLOPE model best explained chorus frog abundance during the first year. Chorus frogs were negatively associated with both variables, and no other models received high AIC support. Both fish abundance and slope had individual variable weights of 0.99. During the second year, FISHVEG replaced FISHSLOPE as the best model. Chorus frogs were again negatively associated with fish abundance, but they were also positively associated with vegetation cover. The individual variable weight for fish was again very high ( $w = 0.99$ ) with vegetation cover a close second ( $w = 0.97$ ). The global model for the second year was the second most highly ranked model in the set ( $W = 0.28$ ,  $\Delta AIC = 1.8$ ). Chorus frogs were again negatively associated with steep wetland slopes, but this relationship was not highly ranked by our AIC analyses. Only 366 of the 18 362 chorus frog metamorphs captured during the second year emerged from steep-sloped wetlands.

Bullfrog metamorph production occurred only in 2008, and although low, production was best explained by a negative association with VEG. The VEGSLOPE model also had high support ( $\Delta AIC = 0.68$ ) and vegetation cover had the highest individual variable weight ( $w = 0.87$ ).

The global models for the 2008 captures of northern cricket frogs and green frogs did not fit the data (cricket

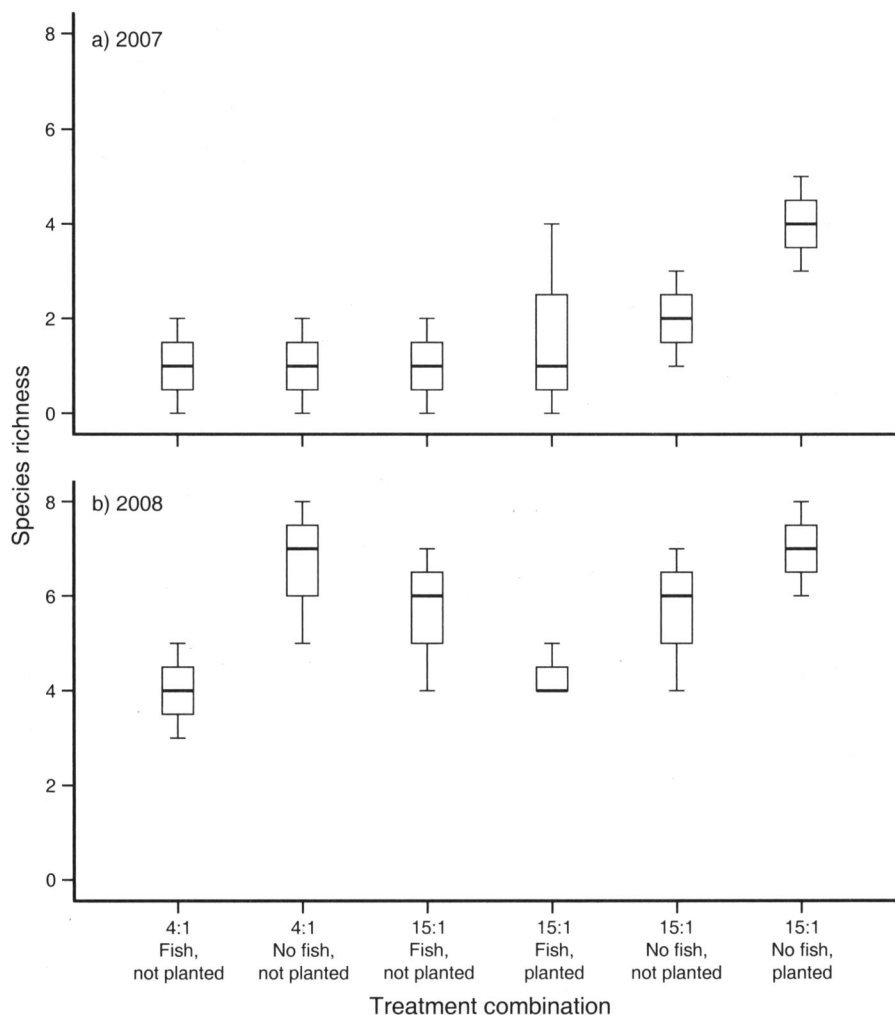


FIG. 4. Boxplots illustrating species richness for each wetland treatment combination and slope. The top and bottom of the boxes represent the interquartile range (50% of the cases), the line within the box is the median, and the whiskers represent the entire range.

frog,  $\chi^2 = 4.2$ ,  $df = 3$ ,  $P = 0.25$ ; green frog,  $\chi^2 = 4.8$ ,  $df = 3$ ,  $P = 0.19$ ), and because smallmouth salamanders and spring peepers were captured in only two and three wetlands, respectively, we did not conduct AIC analyses for these species.

#### Species richness

Species richness increased across all of the wetland treatment combinations from 2007 to 2008 (Fig. 4). The global models for species richness fit the data and were significant in both years (both  $P \leq 0.005$ ). Species richness during the first sampling year was best explained by the FISHVEG model. Richness was negatively associated with fish abundance but positively influenced by the presence of planted vegetation. Vegetation had the highest individual variable weight ( $w = 0.95$ ) followed by fish ( $w = 0.92$ ). For the 2008 data, FISHVEG was again the highest ranking model explaining species richness. The FISH model was the

second highest ranked and also had a high individual variable weight ( $w = 0.83$ ). Vegetation cover was also relatively important in the 2008 model set ( $w = 0.66$ ).

#### Metamorph quality

Hierarchical linear regression analyses revealed little influence of the wetland design features on average toad and chorus frog metamorph size. Models for both species had percentage of explained variances of  $< 1$  and no significant relationships (all  $P > 0.5$ ). The results for leopard frogs were stronger. Mosquito fish abundance, slope, and vegetation cover entered in step 1 of the model and explained 34.8% of the variance based on adjusted  $R^2$ . After adding leopard frog metamorph production in step 2, the total variance explained by the model was 52.2%,  $F_{4,11} = 5.1$ ,  $P = 0.01$ . Leopard frog metamorph production explained an additional 17% of the variance (change in  $F$ ),  $F_{1,11} = 5.37$ ,  $P = 0.04$ . In the final model, only slope ( $\beta = 0.67$ ,  $P = 0.004$ ) and leopard

frog metamorph production ( $\beta = -0.42$ ,  $P = 0.04$ ) had statistically significant influences on size.

#### DISCUSSION

As biodiversity continues to be lost, experimental conservation biology can be an important tool for revealing methods to increase diversity and improve restoration practices. While our research highlights the importance of littoral zone slope, vegetation, and fish abundance for amphibians, the wetlands have also provided habitat for other taxa, and opportunities to examine the effects of design features on development of other communities. Our study not only illuminates the alternative pathways of ecological succession when different aquatic features are used by restoration ecologists, it also highlights the consequences of introducing mosquito fish into wetland restoration practices.

Wetland design directly influences amphibian species richness, reproductive success, and assembly of the amphibian community. Incorporating shallow littoral zones and encouraging vegetation maximizes amphibian colonization and bolsters reproductive output. We found that the reproductive success of leopard frogs, toads, and chorus frogs was highest in shallow-sloped wetlands during the first year, and this trend continued for toads and chorus frogs during the second year. Planted vegetation was also important for bolstering leopard frog metamorphs during the first year. Chorus frogs and gray tree frogs were almost exclusively produced at fish-free wetlands during both years, and amphibian diversity was highest in shallow-sloped, fish-free wetlands with high vegetation cover.

#### *Metamorph production*

During the first year post-construction, amphibian production at the wetlands was predictably dominated by early colonizers. These species are adapted to seasonal temporary wetlands that have low predator loads, and their larvae actively search for resources (Skelly 1995). Therefore, at this early stage of wetland development, cover may not be as essential as access to food such as algae and phytoplankton that develop in the shallow, highly illuminated littoral zones. Sunlight is also important for thermoregulation, allowing larvae to maximize metabolic activity and growth so that metamorphosis occurs before wetlands dry. Because of their high activity levels, larvae of early colonizers would be vulnerable to predation without some defense mechanism (i.e., unpleasant taste or altered behavior). Unless introduced, new constructed wetlands (regardless of their designed hydroperiods) contain few predators during the first year. Some early-colonizing amphibians, such as chorus frogs and gray tree frogs, may first avoid wetlands containing predators and then select wetlands that contain features that maximize growth and lower the time to metamorphosis.

Breeding adult amphibians are capable of actively avoiding wetlands with fish (Binckley and Resetarits 2008). During early spring reconnaissance visits, loud diurnal choruses of *P. maculata* were often heard in and around the fish-free experimental wetlands, particularly those with shallow slopes, but none were heard in and around those stocked with fish (C. D. Shulse, *personal observation*). Because some chorus frog metamorphs emerged from fish-stocked sites, low numbers of breeding adults may have selected wetlands with fish during peak breeding activity to avoid intraspecific larval competition (Binckley and Resetarits 2008). American toads, on the other hand, are unpalatable to fish (Kats et al. 1988), and appear to prefer wetlands with shallows regardless of fish presence; a finding consistent with Porej and Hetherington (2005).

Our results indicate that there is a significant negative impact of *Gambusia* stocking on total amphibian reproductive success, but this was only apparent the first year. This was likely due to the high numbers of toads produced at a fish-free wetland during 2007. This trend did not continue in the second year, as the highest number of toads was produced at a fish-stocked wetland. The eggs of early-colonizing hyloid species that usually breed in temporary wetlands may be more palatable to mosquito fish than leopard frogs or toads that often reproduce in both permanent and temporary sites (Grubb 1972).

Within-wetland slopes were the best predictor of total amphibian metamorph production during the first year post-construction. Reproductive success was greatest in wetlands with shallow slopes, and while this trend continued during the second year post-construction, our results illustrate that vegetation cover surpasses shallow slopes as a factor driving amphibian production. This suggests that the benefits provided by shallows alone may become somewhat less important as vegetation structure develops. Nevertheless, from an economic standpoint, constructing wetlands with extensive shallows requires less excavation and labor than steep-sloped ponds and may provide amphibians with important habitat early, particularly prior to the establishment of vegetation. As wetlands age and succession proceeds, vegetation likely plays a vital role in providing cover and oviposition substrates for later colonizers. However, in our study, bullfrog production was lower in wetlands with high vegetation cover. This result may reflect avoidance by breeding adults or increased larval mortality in habitats with large predatory aquatic insect populations that may be bolstered by high vegetation (Stewart and Downing 2008, Shulse 2011). Alternatively, our results may be a reflection of the low number of bullfrog metamorphs detected, and captures that were almost exclusively within one of the three wildlife areas. The second highest number of bullfrog metamorph captures occurred in a wetland with no vegetation. Therefore, our results for bullfrogs should be considered preliminary until additional data are collected and analyzed.

### *Species richness*

AIC analyses of species richness regression models gave consistent results for both sampling years. Negative associations with fish and positive associations with vegetation highlight the importance of predator avoidance through breeding site selection and cover. However, the importance of each of these variables reversed between sampling years. During the first year, the planted vegetation clearly bolstered amphibian richness. All detected species produced metamorphs at planted wetlands, and leopard frog egg masses were often observed attached directly to prairie cordgrass stems. During the second year, mosquito fish abundance became more important than vegetation cover in driving amphibian species richness. Breeding adult chorus frogs and gray tree frogs continued to largely avoid fish-stocked wetlands, keeping their diversity low. However, leopard frogs became nearly ubiquitous during the second year, as almost every wetland had developed some vegetation structure.

Previous studies have yielded contradictory results regarding the benefits of vegetation for amphibians leading to differing management recommendations. For example, Knutson et al. (2004) found that multi-species reproductive success was highest in ponds with less emergent vegetation, and Porej and Hetherington (2005) found no relationship between species richness and emergent vegetation cover alone. However, Hazell et al. (2004) and Hartel et al. (2007) found that pond occupancy of some amphibians, as well as species richness, were higher in ponds with high vegetation cover. In a previous study, we found that abundances of some amphibians in northern Missouri constructed wetlands were positively associated with vegetation cover (Shulze et al. 2010). The results of our wetland experiments agree with those of the latter field studies that found positive benefits of vegetation for amphibians. While the benefits in the first year appeared to have been strong only for leopard frogs, weaker interactions with other species should not be discounted. Chorus frogs and gray tree frogs also attach their egg masses to twigs and grasses (Johnson 2000), and the amount of vegetation added may be a factor in the number of egg masses deposited. During the first year, vegetation was a resource limited to a few wetlands, but by the second year, this resource became widespread throughout most wetlands as our vegetation cover *t* tests indicated. Future studies should attempt to determine if vegetation is a limiting factor for breeding and oviposition, and to identify the ideal species and amounts of vegetation to add to restored wetlands.

Although we did not identify all of the plants that colonized our wetlands, we did not notice any nonnative invasive species. Cattails (*Typha* sp.), arrowheads (*Sagittaria* sp.), and spikerushes (*Eleocharis* sp.) appeared to be the most common emergent vegetation, while floating and submerged pondweeds (*Potamogeton* sp.) also became established in some wetlands. Nonnative wetland plants may negatively impact amphibians

(Brown et al. 2006), but additional studies are needed to more fully understand how changes to vegetation structure from invasive wetland flora affect amphibians. Nonetheless, the benefits amphibians garner from vegetation structure as refuge from predatory macroinvertebrates and most fish species may not translate to effective refuge from mosquito fish. These small fish forage in the shallow, heavily vegetated littoral areas of wetlands where many larval amphibians congregate (Baber and Babbitt 2004), exposing larvae to elevated levels of predation and sublethal injuries (Shulze 2011).

### *Metamorph quality*

Our analyses revealed little influence of the treatment variables on metamorph quality for toads and chorus frogs. However, the average size of leopard frog metamorphs was greater in wetlands with steep slopes and lower numbers of leopard frogs. Wetlands with lower densities of cohorts likely contributed to reduced competition for resources resulting in larger size at metamorphosis. The steep-sloped wetlands had greater water volumes and may have allowed overwintering leopard frog larvae to better survive winter conditions and reach greater sizes at metamorphosis the following spring. Additionally, wetlands with shallows that have higher light and food levels may result in faster growth, whereas larvae in steep-sloped wetlands may have developed more slowly, resulting in greater size at metamorphosis (Berven and Gill 1983). Habitat size has been shown to influence the fitness of larval anurans (Pearman 1993, 1995) and although our wetlands all had the same surface area, substrate and water column differences between the two designs may have contributed to differences in leopard frog metamorph size. However, due to our limited data set, our results should be considered preliminary, and further investigation is necessary to elucidate the influences of wetland design on metamorph quality.

### *Broader restoration implications*

Immediately following construction, restoration sites begin the process of ecological succession. Many factors determine the pathways of succession. Although attempts are made to expedite these processes, for example, through the introduction of flora and fauna, predicting the outcome of restoration is fraught with pitfalls due to a lack of science-based experimentation (Zedler 2000). Our study contributes to wetland construction practices that benefit amphibians because we assess three features experimentally that past observational studies have shown to be important wetland components for predicting amphibian occurrence, abundance, and species richness (e.g., Hazell et al. 2004, Porej and Hetherington 2005, Hartel et al. 2007, Shulze et al. 2010). Our study goes beyond previous investigations by constructing wetlands that directly test relationships between amphibians and the features of interest, while attempting to control for other confounding variables. However, many factors that we did not alter, and some that we could not

control, likely played important roles in the development of the observed amphibian communities and their reproductive success. For example, hydroperiod is a fundamental characteristic that helps to determine wetland floral and faunal communities. Our wetlands were consistently filled with water for the duration of our study, and they have continued to remain filled, probably because the region experienced higher than normal precipitation (>127 cm) in both 2008 and 2009 (annual average was 89–102 cm; National Weather Service).

Consistently permanent hydroperiods likely contributed to the development of amphibian communities in all of the wetlands, consisting of large ranid species that require permanent water (see Shulse et al. 2010). Breeding boreal chorus frogs largely abandoned the wetlands by the third year (2009), perhaps because of high populations of predatory aquatic macroinvertebrates (see Shulse 2011) and potential competition or predation from ranid larvae (Faragher and Jaeger 1998, Boone et al. 2008). Wetland substrates also influence abiotic conditions (i.e., pH, total cations, organic carbon) and biotic conditions (i.e., vegetation development) that, in turn, may affect amphibian communities. Differences in wetland substrate, particularly between sites, could have influenced development of amphibian communities. Future studies should examine amphibian community development in wetlands constructed in different substrates, and in wetlands with different hydroperiods and water volumes.

Our results represent short-term amphibian community succession during the first two years after wetland construction. Longer-term studies would aid our understanding of the influences of the effects of the experimental variables in more mature wetlands. However, we hypothesize that hydroperiod will likely be a primary regulator of amphibian communities within our experimental wetlands in future years. While predators also shape amphibian communities, aquatic insects and fish are themselves regulated by hydroperiod and cannot persist in wetlands that dry and refill periodically. This form of disturbance enhances reproductive success for early-colonizing amphibian species. Intermittent drying and filling is an important element of many natural wetlands, and compensatory mitigation wetlands should reflect the natural hydroperiods of the wetlands that they attempt to replace. Multiple restoration projects within a region should reflect the natural diversity of wetland hydroperiods required to sustain diverse regional communities and reduce local extinction risks (Semlitsch and Bodie 1998, Petranka et al. 2007, Shoo et al. 2011).

Although many studies have shown that fish are detrimental to some amphibians (e.g., Kats et al. 1988, Snodgrass et al. 2000, Pope 2008, Hamer and Parris 2011), researchers investigating amphibian declines often overlook the role of alien fish species purposely spread by humans for various ornamental, recreational, or biological control measures. Studies have revealed the deleterious effects of several introduced fish taxa on

native amphibian populations (Kats and Ferrer 2003, Leu et al. 2009, Bowerman et al. 2010). *Gambusia affinis* warrants special attention, not only because of its pervasive use, ease of spread, and ability to survive a wide range of aquatic conditions, but also because of the widespread perception that it is benign to native wildlife (Pyke 2008). While stocking *Gambusia* may initially seem “environmentally friendly,” our results provide further evidence that these invasive fish harm native amphibian species and undermine restoration efforts. Furthermore, these fish likely reduce macroinvertebrate density and diversity (Blaustein 1991, Schaefer et al. 1994, Lawler et al. 1999). Wetland managers should not release mosquito fish into water bodies where they are alien, and stakeholders should be educated about their detrimental effects on native ecosystems. We are not suggesting that mosquito control efforts to protect human health should be terminated. Preferable alternatives to *Gambusia* that also feed upon larval mosquitoes are larvae of native salamanders (Brodman et al. 2003, DuRant and Hopkins 2008) and many aquatic invertebrates (Laird 1977). The colonization of these taxa in constructed wetlands should be encouraged by providing appropriate habitats free of *Gambusia*.

The introduction or proliferation of invasive species in disturbed areas can lead to “novel ecosystems” with unnatural species combinations that complicate restoration efforts (Hobbs et al. 2006). Adding an alien species (regardless of intention) can dramatically affect ecological succession pathways by reducing reproductive success and/or excluding native species. Additionally, simple adherence to the “build it and they will come” philosophy of restoration ignores ecological succession and alternative stable states. Both are dangerous practices for planners and managers because how restoration sites are built dictates who “they” are, while site maintenance and natural succession determine species that remain, and those that later colonize. We challenge restoration ecologists to conduct more applied experimental investigations that lead to a better understanding of successional and maintenance processes for constructed wetlands. Results of these experiments should be made available to planners, managers, and researchers so that the knowledge gained can be incorporated into future projects.

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#### SUPPLEMENTAL MATERIAL

##### Appendix A

Experimental wetland designs illustrating dimensions, within-wetland slopes, and plant placement (*Ecological Archives* A022-089-A1).

##### Appendix B

Table summarizing the number of metamorphs of each species captured at all wetland treatment combinations for both sampling years (*Ecological Archives* A022-089-A2).

##### Appendix C

Complete model selection results for AIC<sub>c</sub> analyses (*Ecological Archives* A022-089-A3).