

Restoring diversity after cattail expansion: disturbance, resilience, and seasonality in a tropical dry wetland

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Abstract. As the human footprint expands, ecologists and resource managers are increasingly challenged to explain and manage abrupt ecosystem transformations (i.e., regime shifts). In this study, we investigated the role of a mechanical disturbance that has been used to restore and maintain local wetland diversity after a monotypic regime shift in northwestern Costa Rica [specifically, an abrupt landscape-scale cattail (*Typha*) expansion]. The study was conducted in Palo Verde Marsh (Palo Verde National Park; a RAMSAR Wetland of International Importance), a seasonally flooded freshwater wetland that has historically provided habitat for large populations of wading birds and waterfowl. A cattail (*T. domingensis*) expansion in the 1980s greatly altered the plant community and reduced avian habitat. Since then, *Typha* has been managed using a form of mechanical disturbance called fanguero (a Spanish word, pronounced “fahn-gay-yo” in English). We applied a *Typha* removal treatment at three levels (control, fanguero, and fanguero with fencing to exclude cattle grazing). Fanguero resulted in a large reduction in *Typha* dominance (i.e., decreased aboveground biomass, ramet density, and ramet height) and an increase in habitat heterogeneity. As in many ecosystems that have been defined by multiple and frequent disturbances, a large portion of the plant community regenerated after disturbance (via propagule banking) and fanguero resulted in a more diverse plant community that was strongly dictated by seasonal processes (i.e., distinct wet- and dry-season assemblages). Importantly, the mechanical disturbance had no apparent short-term impact on any of the soil properties we measured (including bulk density). Interestingly, low soil and foliar N:P values indicate that Palo Verde Marsh and other wetlands in the region may be nitrogen limited. Our results quantify how, in a cultural landscape where the historical disturbance regime has been altered and diversity has declined, a mechanical disturbance in combination with seasonal drought and flooding has been used to locally restrict a clonal monodominant plant expansion, create habitat heterogeneity, and maintain plant diversity.

Key words: clonal plant; Costa Rica; invasive plant management; mechanical disturbance; nitrogen limitation; N:P stoichiometry; Palo Verde National Park; regime shift; seasonal flooding and drought; seed bank; *Typha domingensis*; wetland restoration.

INTRODUCTION

In the last several decades, human actions have been increasingly linked to abrupt and dramatic ecosystem transformations across large spatial scales in a variety of terrestrial, aquatic, and marine ecosystems (i.e., regime shifts [Scheffer and Carpenter 2003, Folke et al. 2004]). Since these transformations greatly alter the structure and functioning of ecosystems and the support of important ecosystem services, there has been much discussion about appropriate approaches for managing these transformed ecosystems and the potential for restoration after a regime shift (Suding et al. 2004, Hobbs and Suding 2009). Regime shifts often produce

ecosystems with positive feedbacks and properties that enhance stability and resilience. As a result, ecosystem management after a regime shift is sometimes unpredictable and often entails the development and application of innovative approaches (Suding et al. 2004, Seastedt et al. 2008, Hobbs et al. 2009). In this study, we investigate the role of a mechanical disturbance-based management approach (called fanguero; description in subsequent paragraphs) that has been used to restore and maintain diversity after a monotypic regime shift (specifically an abrupt landscape-scale cattail expansion) in northwestern Costa Rica. Our investigation examines the impact of repeated disturbance and seasonality on the plant community in an ecosystem where high diversity has historically been maintained by multiple and frequent disturbances.

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Globally, cattail species are among the most ubiquitous, competitive, and invasive emergent plants in freshwater wetland ecosystems. The rapid expansion of cattail (*Typha* spp.; Typhaceae) into wetlands historically not dominated by cattail has occurred across the globe in response to various natural and anthropogenic perturbations (e.g., nutrient enrichment, altered hydroperiod, reduced salinity, altered sedimentation rates, non-native genotype introductions) (Galatowitsch et al. 1999, Zedler and Kercher 2004, Richardson 2008a, Travis et al. 2010). Many of these cattail expansions have occurred fast enough and at a large enough scale to be called regime shifts (see Gunderson 2001, Hagerthey et al. 2008). Due to *Typha*'s potential for rapid dispersal, establishment, and clonal growth, in combination with the positive feedbacks associated with high litter production (Farrer and Goldberg 2009, Tuchman et al. 2009, Vaccaro et al. 2009), *Typha* expansion typically produces stable monodominant plant communities that support different ecosystem functions and services than those present prior to expansion (Richardson 2008a). During cattail expansion, *Typha* can be both the passenger of change (i.e., invasion caused primarily by environmental change with minimal species interaction) and the driver of change (i.e., invasion caused primarily by species interactions with subsequent environmental change; see discussion in Farrer and Goldberg [2009]) (sensu MacDougall and Turkington 2005). Hence, efforts to manage cattail are often complex and have challenged natural resource managers for many decades (Nelson and Dietz 1966, Linde et al. 1976, Apfelbaum 1985, Kostecke 2002). There is much interest in novel approaches that can be used at the local level to reduce the dominance of monodominant clonal plants like *Typha*, increase diversity, and restore wetland ecosystem conditions.

The freshwater wetlands within and adjacent to Palo Verde National Park (PVNP; northwestern Costa Rica) are among the most ecologically important and diverse wetland complexes in Central America; together, these wetlands have been designated a Ramsar Wetland of International Importance, primarily due to the important habitat that they have historically provided for large concentrations of waterfowl and wading birds. We refer to these wetlands as tropical dry wetlands to highlight the climatic drivers that shape these ecosystems (specifically distinct and extreme seasonal flooding and drought; for readers who might be more familiar with tropical dry forests, these wetlands occupy the lower portions of the same landscapes that contain tropical dry forests [Holdridge 1967]). In the 1980s, a regime shift occurred within a large freshwater wetland in PVNP (Palo Verde Marsh) that greatly altered the historic wetland regime and the habitat available to support avian populations. The historic regime (a heterogeneous landscape containing patches of open water, free-floating and floating-rooted aquatic vegetation, and predominantly short emergent vegetation [see McCoy

and Rodriguez 1994, Trama 2005, Trama et al. 2009]) was rapidly converted to an expansive cattail monoculture. The cause of the sudden and dramatic *Typha* expansion has most often been attributed to a reduction in cattle grazing (i.e., the cattle actually eat young *Typha* shoots and trample vegetation; thus, this hypothesis contends that cattle grazing prevented competitive exclusion [McCoy and Rodriguez 1994, Burnidge 2000]). Although this is a plausible explanation and similar results have been observed in several other seasonally flooded and historically grazed tropical wetlands (Middleton 1999), rigorous tests of this hypothesis at Palo Verde Marsh have never been implemented and debate regarding the importance of grazing intensity continues. Furthermore, historic abiotic conditions throughout the watershed were also greatly altered during this period (see discussions in Peters [2001], Trama [2005], Daniels and Cumming [2008], Powers et al. [2009]), and other potential causal factors that have been mentioned but not conclusively examined include altered hydroperiod (González 2002, Jiménez et al. 2003), reduced salinity, increased nutrient inputs, altered fire regimes, and *Typha* hybridization.

In grasslands and other cultural landscapes throughout the world, repeated disturbance in the form of mowing and grazing is often used to simulate historic herbivory rates, reduce the biomass of competitive dominant tall plants, and increase plant diversity (Collins et al. 1998, Bakker and Berendse 1999, Maron and Jefferies 2001). Annual mowing is used effectively to remove plant biomass and increase plant diversity in many European floodplains (Grootjans et al. 2002, Gerard et al. 2008). In Central Mexican wetlands, *T. domingensis* is repeatedly harvested for weaving, fodder, and fertilizer, a sustainable process that results in higher plant diversity and a source of income for local communities (Hall et al. 2008, Hall 2009). In Palo Verde Marsh, *Typha* has been managed with a unique form of repeated disturbance called fanguero (a Spanish word, pronounced "fahn-gay-yo" in English). Fanguero is a mechanical disturbance technique used locally in northwestern Costa Rica during rice farming to control weeds and also reduce water infiltration via increased soil compaction. See McCoy and Rodriguez (1994) for a discussion of how the fanguero method was first used to restrict *Typha* expansion in PVNP wetlands. In the context of this study, we use the term fanguero to refer to the use of a tractor with metal paddle wheels to crush and locally remove *Typha* in standing water (see photographs in Fig. 1a, b, c). During the first pass of a fanguero tractor, *Typha* ramets are crushed and crimped, which limits oxygen transport (McCoy and Rodriguez 1994). During subsequent passes, the *Typha* ramets and parts of the rhizome are typically pulled up, temporarily dragged behind the tractor, and locally removed. After fanguero treatment, stresses associated with lack of oxygen due to flooding during the wet season and a lack of water availability during the dry season will



FIG. 1. Photos from Palo Verde Marsh, Palo Verde National Park, Costa Rica, depicting: (a, b) a tractor with metal paddle wheels used to remove *Typha* via a mechanical disturbance that is called fanguero; (c) the edge of a plot where *Typha* was removed via fanguero, and (d) migratory birds utilizing and flying away from a plot where *Typha* was removed via fanguero. Most of the individuals in the last photo are Black-bellied Whistling Ducks (*Dendrocygna autumnalis*), which were especially numerous after *Typha* removal (photo credits: M. J. Osland).

typically lead to *Typha* mortality. The visual impact of fanguero on avian visitation, aerial cover classes, and the creation of desirable avian habitat in PVNP is dramatic and extremely effective (McCoy and Rodriguez 1994, Trama 2005, Trama et al. 2009) (see Fig. 1d). Yet, as in most *Typha* removal efforts, an intensive field-based assessment of the impact of fanguero on the plant community, *Typha* dominance, and other ecosystem properties has not been conducted.

In this investigation we tested the following hypotheses related to the potential for restoring diversity after cattail expansion in Palo Verde Marsh: (1) the physical disturbance and potential compaction associated with fanguero (i.e., tractor use in a wetland) will have a detrimental impact on soil properties and seedling emergence; (2) management via a novel form of mechanical disturbance (fanguero) will rapidly reduce cattail dominance in the short term (i.e., the first year); (3) since the historic plant community has been shaped by frequent disturbances and distinct and extreme seasonal flooding and drought cycles, the previous plant community contains regenerative properties (i.e., a propagule bank) that will enable rapid reestablishment

of a diverse plant community in response to *Typha* removal and seasonal hydrology (i.e., flooding and drawdown); and (4) the rapid landscape-scale cattail expansion has enhanced cattail stability and resilience, and despite a dramatic short-term decrease in *Typha* dominance and an increase in plant diversity, *Typha* will eventually (e.g., after 2–4 years) reestablish in the absence of additional restorative efforts (e.g., repeated disturbance). To test these hypotheses, we measured the impact of fanguero on several important soil physical and chemical properties and seedling emergence. We also quantified the impact of *Typha* removal on the plant community with an emphasis on the impact of seasonality and measurements that relate to *Typha* resistance and resilience (i.e., *Typha* seed bank, in situ recruitment, vertical growth, and clonal expansion).

METHODS

Study site

This study was conducted in Palo Verde Marsh, within PVNP. PVNP is located in the Province of Guanacaste in the lowlands of the Tempisque River

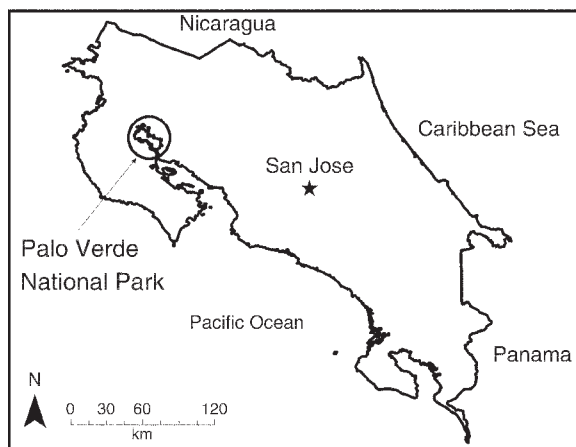


FIG. 2. Map of Costa Rica identifying the location of Palo Verde National Park.

Watershed in northwestern Costa Rica (Fig. 2). The climate in this part of Costa Rica is tropical and very seasonal. The wetlands of PVNP are collectively designated a RAMSAR Wetland of International Importance and cover an estimated 9880 ha of the total 18 800-ha area included in the park (J. Serrano, *personal communication*). The Organization for Tropical Studies (OTS) manages a biological station (Palo Verde Biological Station) which is within the park and immediately adjacent to Palo Verde Marsh.

Ecosystem processes in the region's freshwater wetlands are defined by seasonal flooding and drawdown associated with wet and dry seasons. Palo Verde Marsh (~1250 ha; 10°20'35" N, 85°20'25" W), fills with water during the wet season (~May–November) to a typical maximum depth of ~1.5 m. Most of these hydrologic inputs are due to surface water runoff from the adjacent forest during the wet season. However, in some years, tropical storm activity at the end of the wet season (typically in September or October) will produce water levels in excess of 1.5 m at the site as the Tempisque River rises higher than the natural levees and causes widespread flooding. During the dry season (~December–May), the water level gradually recedes due to high evapotranspiration rates that exceed the rainfall. At the end of the dry season, much of the wetland has no standing water. However, small precipitation events during the last few months of the dry season (March–April) in some years will delay and sometimes prevent complete drawdown in the wetlands. The soils in most of the wetlands within and adjacent to PVNP (including Palo Verde Marsh) are Vertisols (Loaiciga and Robinson 1995), which expand in the wet season and contract during the dry season, forming a relatively uniform and deep A horizon. Extensive cracking during the dry season (especially in areas without vegetation) promotes the mixing of this layer as pieces from the surface fall into cracks. The shrink–swell qualities of Vertisols typically enable them to recover

from compaction (Sarmah et al. 1996). At present, the soil properties at the site are not well documented in the literature.

The range in total annual precipitation at the site is large. Between 1997–2007, the mean \pm SE, minimum, and maximum annual cumulative precipitation for a hydrologic year (April–March) were 1271 \pm 131 mm, 717 mm, and 2201 mm, respectively (data obtained from on-site OTS records). For a longer time period (1921–1999), the mean annual precipitation for the entire Tempisque River Watershed was estimated to be 1817 mm (Mateo-Vega 2001). The mean \pm SE annual temperature at the site between 1997 and 2007 was 28.1° \pm 0.3°C. The coldest months were at the end of the wet season (September and October), with a mean temperature of 26.8° \pm 0.2°C. The warmest months were at the end of the dry season (March and April) with a mean temperature of 29.7° \pm 0.2°C.

Experimental design

Since the hydrologic and edaphic spatial variability at the site was unknown when we began the study, and potentially heterogeneous, we selected a randomized complete block design for this investigation. Within 15 blocks, a *Typha* removal treatment was applied at three levels (Control [C], *Typha* removed via fangueo [F], and *Typha* removed via fangueo and plot fenced [FF] to exclude cattle grazing). Whereas the cattail in the C plots was not removed, the cattail in the F and FF plots was removed via fangueo. The FF plots were also enclosed by a barbed wire fence in order to restrict cattle access and assess the additional impact of grazing after fangueo on the vegetation. *Typha* removal via fangueo was conducted in early February 2007. Within each block, the three treatment levels were each randomly assigned to 20-m² plots with at least 5-m buffers on all sides (a total of 45 20-m² plots). Within each 20-m² plot, three 1-m² permanent quadrats were randomly established for vegetation surveys (a total of 135 1-m² quadrats). The relative water depth of each plot was determined during wet-season surveys (Table 1).

Soil

Within each of the C and F 20-m² plots, two soil samples to 10-cm depth were collected during the first month after fangueo. Due to logistical constraints, we did not collect soil samples from the FF plots. One sample was used to determine bulk density (BD) and soil organic matter (SOM), and the other was used for total nitrogen (TN), total carbon (TC), and total phosphorus (TP) analyses. To minimize compaction, soil samples were collected by gently pounding a lightweight stainless steel piston core liner with a sharpened tip into the soil using a 680-g dead blow hammer. After collection, samples were stored at 4°C in sealed plastic bags at the OTS Palo Verde Biological Station until transport to the Duke University Wetland Center for analysis. Samples to be analyzed for TN, TP, and TC were dried,

TABLE 1. A timeline of when the response variables were measured after removal of *Typha* via fangueo.

Response variable	Time of measurement
Soil properties	first month
Seedling emergence	third month (monitored for subsequent five months)
Plant community composition	second, third, and fourth month (first dry season) fifth and eighth month (first wet season) 15th month (second dry season)
<i>Typha</i> dominance and expansion	third month (first dry season) 15th month (second dry season)

homogenized into fine powder via a mixer mill, and passed through a 2-mm sieve. SOM was determined using the loss on ignition method (Karam 1993). TN and TC were measured via dry combustion using a CHN autoanalyzer (McGill and Figueiredo 1993, Tiessen and Moir 1993). TP was measured after nitric-perchloric acid digestion (Sommers et al. 1970) using an automated ascorbic acid method (Murphy and Riley 1962) on a Lachat autoanalyzer (O'Halloran 1993). Soil and *Typha* foliar (i.e., live culms) N:P ratios on a mass basis were calculated to gauge nutrient limitation (Koerselman and Meuleman 1996, Verhoeven et al. 1996, Bedford et al. 1999). We measured the soil pH of a subset of five samples in dilute salt solution (0.01 mol/L CaCl₂) (Hendershot and Lalande 1993).

Seed bank

A seedling emergence experiment was established with the following factors: *Typha* removal via fangueo (using the C and F plots) and water level (drawdown, flooded). Due to logistical constraints, we did not collect soil samples from the FF plots. Two sets of duplicate composite cores were collected from each of the C and F treatment plots. Each composite contained 11 cores (5-cm depth, 4.6-cm diameter each; a total of 660 precomposite cores; total volume and area for each composite sample was 914 cm³ and 183 cm², respectively). Each composite was mixed and placed in a 2-cm layer on top of a 5-cm layer of sterilized potting soil in flats with the following dimensions: 25 cm long × 20 cm wide × 10 cm deep. Each duplicate was assigned to one of two water level treatments: flooded or drawdown. The water level in the flooded flats was maintained 3 cm above the soil surface, and the drawdown flats were kept moist but not flooded. This study was conducted in a lath house at the OTS Palo Verde Biological Station. In order to account for contaminant seeds, eight control trays (i.e., trays with just the 5-cm layer of sterilized potting soil; four drawdown and four flooded) were included in the experimental design. However, we lost two controls due to an iguana that repeatedly defecated from the lath house roof above these trays, preventing any potential germination. Emerging seedlings were identified and counted on seven dates between May and September 2007.

Plant community

Vegetation data were collected within each 1-m² quadrat at various time intervals (Table 1). In order to quantify the postdisturbance *Typha* recruitment potential, the number of *Typha* seedlings present in each 1-m² quadrat was recorded during these vegetation surveys. The cover data were used to calculate species richness and diversity (using the Shannon-Wiener index with the use of the relative percentage cover of species *i* to represent p_i in the calculations). In order to gauge species dominance, we used the percent cover values to calculate importance values (IV), calculated as: IV = (mean percentage cover × frequency)/100. We also calculated seasonal indicator values for the standing vegetation species via indicator species analysis (INSPAN) (Dufrene and Legendre 1997) using PC-ORD Version 4 (MjM Software, Gleneden Beach, Oregon, USA) (McCune and Medford 1999). Indicator values represent the percentage of perfect indication of a species for a given group. In our analyses, indicator values reflect the faithfulness (i.e., constancy of presence; see McCune and Grace 2002) of a species to the dry or wet-season plant community.

Typha ramet density, height, and perpendicular basal diameters were measured within each 1-m² quadrat in April 2007 and 2008. Aboveground *Typha* biomass was determined using an allometric relationship we developed (sensu Miao et al. 2008) using biomass, leaf height, and elliptical basal area measurements from 148 ramets. These measurements produced the following equation ($r^2 = 0.97$) which was used to calculate *Typha* aboveground biomass within each plot.

$$\begin{aligned} \ln(\text{aboveground biomass}) = & -5.729 \\ & + 0.420 \times \ln(\text{basal area}) \\ & + 1.281 \times \ln(\text{height}). \end{aligned}$$

In order to quantify annual cattail horizontal rhizome expansion and gauge the potential for expansion into recently managed areas, 15 10-m permanent transects were established on the edges between the C and F plots. The distance from the edges to the furthest cattail ramet was measured at 2-m intervals during the 2007 and 2008 dry season. However, on two of these transects, cattail recruitment and growth was so extensive that we could not determine the limit of vegetative expansion. Hence,

TABLE 2. Effect of mechanical disturbance (i.e., fangueo) on soil properties (mean \pm SE) at the site.

Soil properties	No mechanical disturbance	Mechanical disturbance
BD (g/cm ³)	1.02 \pm 0.03	0.95 \pm 0.06
SOM (g/kg)	99 \pm 7	108 \pm 14
TC (g/kg)	39.4 \pm 3.8	48.1 \pm 8.3
TN (g/kg)	3.5 \pm 0.3	3.9 \pm 0.6
TP (mg/kg)	529 \pm 53	545 \pm 36
C:N (mass)	11.4 \pm 0.5	12.0 \pm 0.6
N:P (mass)	6.8 \pm 0.5	7.0 \pm 0.9

Note: There was no significant impact of fangueo on any of the properties measured. Key to abbreviations: BD, bulk density; SOM, soil organic matter.

these two transects were not measured and the results from the remaining 13 transects are presented here.

Data analyses

To assess the impact of mechanical disturbance on the measured soil and seed bank dependent variables, we used univariate mixed factor analyses of variance (ANOVA) models with block as a random effect and mechanical disturbance as a fixed effect. For the seed bank analyses, water level was also added to the model as a fixed effect. For the analyses, seed density and soil TP, TN, TC, and SOM were log-transformed to improve normality. The soil and seed bank response variables were only measured for two levels of the *Typha* removal treatment (C and F) and, hence, means were compared using Student's *t* tests.

To compare *Typha* stand characteristic (*Typha* ramet density, height, and aboveground biomass) differences and plant diversity and richness in response to *Typha* removal, we used repeated measures mixed factor effects ANOVA models with the following independent variables: block (random effect), time (fixed effect), *Typha* removal (fixed effect), and the interaction between time and *Typha* removal. *Typha* data were collected from all three *Typha* removal treatment levels for this analysis. So, comparisons of means between treatments within years and between years within treatments were conducted using Tukey's Studentized Range (HSD) tests and repeated measures *t* tests, respectively. All ANOVA analyses were conducted using SAS Version 9.1.3 (SAS 2004).

To illustrate changes in plant community composition due to the *Typha* removal treatments, a nonmetric multidimensional scaling (NMS) analysis (Kruskal 1964, Mather 1976, McCune and Grace 2002) was performed using PC-ORD (McCune and Medford 1999). Prior to analysis, we relativized the species cover data by species maxima and removed rare species, which were defined as species present in <5% of the plots. We also removed one plot survey that had zero plants present. The resultant matrix contained 20 species and 251 plots. Bray-Curtis dissimilarity coefficients were used to quantify plant species compositional distance (Bray and Curtis 1957). In order to determine the

appropriate number of dimensions to include in the analysis, we used a stepdown procedure to compare the number of dimensions with the corresponding change in final ordination stress. We initially evaluated six axes using 100 runs with real data, a stability criterion of 0.00001, a maximum of 400 iterations, and a Monte Carlo test with 300 randomizations to determine whether the resultant axes were stronger than those identified by chance (McCune and Grace 2002). Based upon this procedure, a three-dimensional analysis was deemed optimal and resulted in a final stress of 17.1, a *P* value of 0.001, and a final instability of 0.00001 after 219 iterations. Multi-response permutation procedures (MRPP) were then used to compare the treatment effect on plant community composition within and between dates. For all MRPP analyses, we used Bray-Curtis dissimilarity as the distance measure and $n/(\text{sum } n)$ to weight groups.

RESULTS

Soil

There was no significant impact of mechanical disturbance (i.e., fangueo) on bulk density or any of the soil properties we measured (Table 2). Of the soil properties measured, the blocking factor was only significant for total phosphorus (TP) ($F_{14,14} = 4.3$, $P < 0.01$), which had a wide range in values; the median, minimum, and maximum TP were 473 mg/kg, 357 mg/kg, and 1114 mg/kg, respectively. The soil N:P at Palo Verde Marsh was low (mean \pm SE = 6.9 \pm 0.5) and there was no significant relationship between soil TP and *Typha* aboveground biomass, ramet density, or ramet height. The mean soil pH (in 0.01 mol/L CaCl₂) was 6.5 \pm 0.1.

Seed bank

There was no apparent impact of physical disturbance via fangueo on seed bank germinant density or richness (Fig. 3a, b). As in most wetlands, seed bank germinant density and richness under drawdown conditions was higher than under flooded conditions (Fig. 3a, b; $F_{1,41} = 75.3$, $P < 0.0001$; $F_{1,41} = 51.9$, $P < 0.0001$, respectively). The seed bank in Palo Verde Marsh was both dense and rich (Fig. 3a, b). *Typha domingensis* was one of the most common species in the seed bank at the site; for the drawdown treatment, the *T. domingensis* seed bank germinants accounted for 23% of the total number of germinants. The mean *T. domingensis* seed bank germinant density was 456 \pm 61 germinants/m².

Typha biomass, ramet architecture, recruitment, and clonal expansion

As expected, *Typha* removal via fangueo resulted in a dramatic decrease in *Typha* aboveground biomass (ABG), ramet height, and ramet density during the first year (Fig. 4a, b, c; $F_{2,28} = 229.1$, $P < 0.0001$; $F_{2,28} = 704.4$, $P < 0.0001$; $F_{2,28} = 227.5$, $P < 0.0001$, respectively). However, post-removal *Typha* recruitment

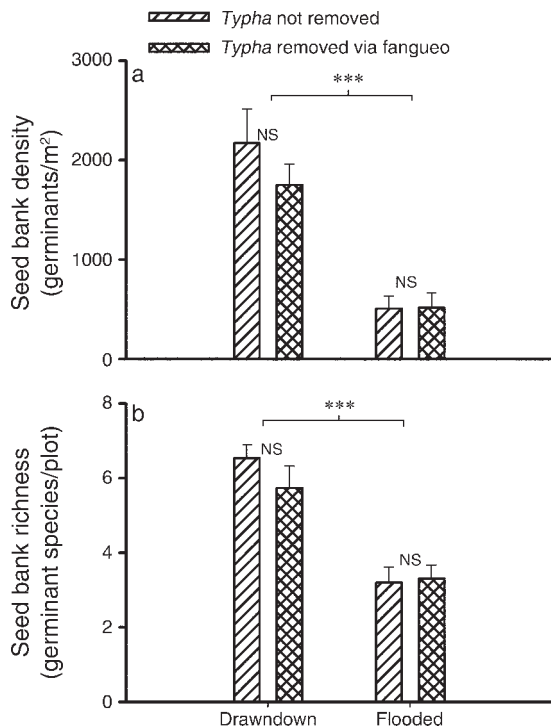


FIG. 3. Impact of mechanical disturbance (i.e., fangueo) and water level on seed bank (a) density and (b) richness (mean + SE).

*** $P < 0.001$

and growth at the site was high (Fig. 4a, b, c) and resulted in significant increases in *Typha* ABG, height, and density in the *Typha*-removed plots (F and FF treatment levels) in the second year (Fig. 4a, b, c; $F_{1,42} = 13.9, P < 0.001; F_{1,42} = 21.5, P < 0.0001; F_{1,42} = 14.7, P < 0.001$, respectively). Despite this increase, *Typha* ABG, height, and density in the *Typha*-removed plots in the second year were still lower than in the control plots (Fig. 4a, b, c; $F_{2,28} = 43.3, P < 0.0001, F_{2,28} = 76.9, P < 0.0001; F_{2,28} = 24.5, P < 0.0001$, respectively). Throughout the study, there was no significant difference between the two *Typha*-removed treatment levels (F and FF) in *Typha* ABG, height, or density (Fig. 4a, b, c). Most of the mature *Typha* stands in our study area were between 2 and 4 m tall, with ramet densities typically in the 9–14 ramets/m² range. However, there are other sections of the Park (e.g., La Bocana Marsh) that have *Typha* stands with ramets that are >5 m in height.

Recently germinated *Typha* seedlings were observed in the *Typha*-removed plots during the March and April 2007 vegetation surveys. *Typha* recruitment in these plots was highest in April 2007 with a mean of 84 ± 20 individuals/m² and a maximum of 368 individuals/m². *Typha* horizontal clonal expansion in the second year along the edge between control and fangueo plots was also high, with a mean expansion of 247 ± 41 cm/yr and a maximum of 571 cm/yr.

Plant community

Typha removal via fangueo resulted in higher plant species diversity (Shannon H') and richness (Fig. 5a, b; $F_{2,221} = 162.3, P < 0.0001; F_{2,221} = 54.6, P < 0.0001$, respectively). Both diversity and richness were higher during the wet-season surveys than the dry-season surveys (Fig. 5a, b; $F_{5,221} = 21.0, P < 0.0001; F_{5,221} = 74.0, P < 0.0001$, respectively). Throughout the study, there was no difference in plant species diversity between the two *Typha*-removed treatment levels (F and FF; Fig. 5a). However, the fenced plots (FF) had a slightly higher plant richness than the unfenced plots (F) (Fig. 5b; $F_{1,138} = 10.1, P = 0.002$), and this difference was greatest during the months of May and June (Fig. 5b; $F_{4,138} = 3.2, P = 0.016$).

There was no significant difference between the plant community composition in the *Typha*-removed treat-

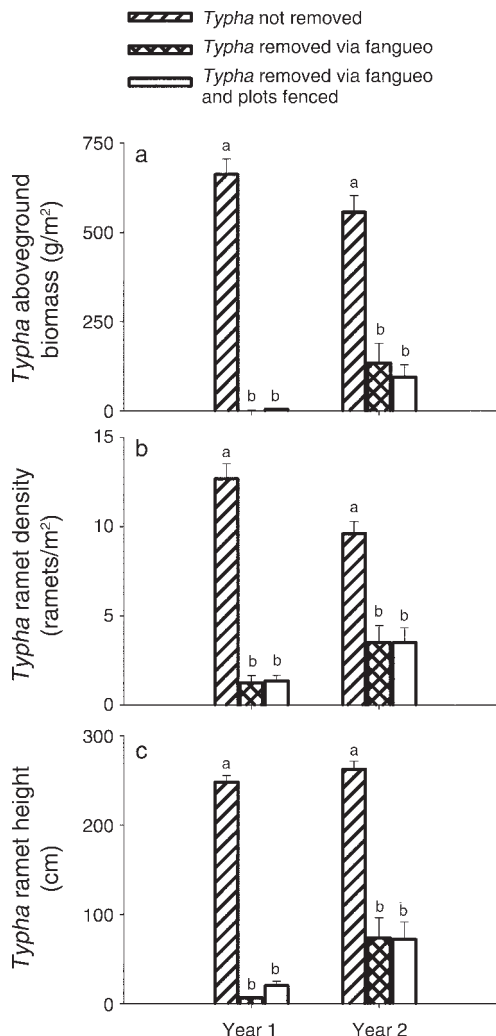


FIG. 4. Impact of *Typha* removal via fangueo and fenced plots on *Typha* (a) aboveground biomass, (b) ramet density, and (c) ramet height (mean + SE). Different letters indicate significant differences between treatments within each year.

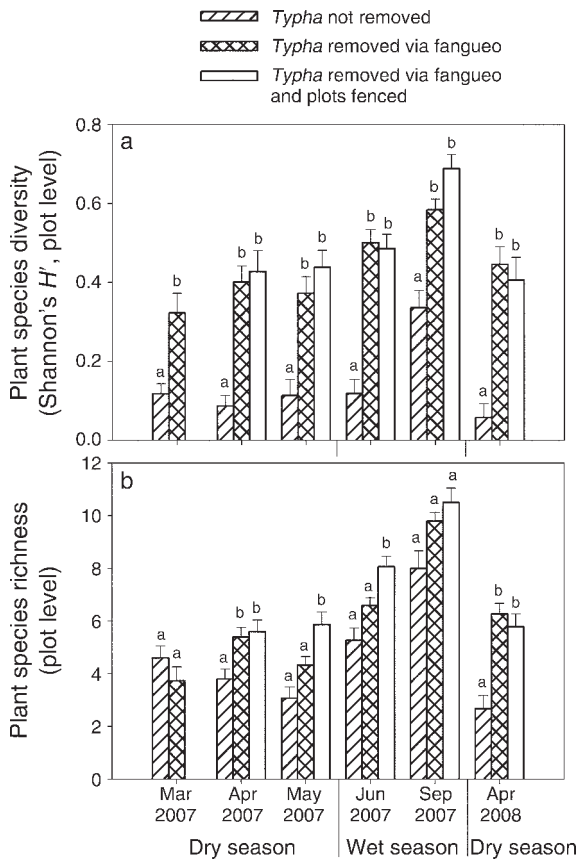


FIG. 5. Impact of *Typha* removal via fangueo and fenced plots on plant species (a) diversity and (b) richness (mean + SE). Letters refer to comparisons between treatments within each sampling period.

ments (F and FF) at any single date in the study (MRPP, $A < 0.02$ and insignificant P for all tests; A is the “chance-corrected within-group agreement” [McCune and Grace 2002]). Hence, these two treatments are illustrated as one group (*Typha* removed via fangueo) in the NMS ordination (Fig. 6). The proportion of the compositional variance represented by the three axes included in the analysis was 0.619 (axis 1, 0.167; axis 2, 0.265; and axis 3, 0.187). Although we tested various environmental variables (i.e., soil properties, elevation, bare ground, litter cover, water depth), water depth was the only variable we measured that was strongly correlated to the biplot axes. Water depth was most strongly correlated to the vertical biplot axis ($\tau = 0.48$).

As expected, the plant community in the *Typha* removed via fangueo plots (F) was significantly different than in the control plots (C) immediately after fangueo (MRPP, March 2007, $A = 0.28$, $P < 0.0000001$) and throughout the course of this study (MRPP, April 2007, $A = 0.29$; May 2007, $A = 0.30$; June 2007, $A = 0.27$; September 2007, $A = 0.26$; April 2008, $A = 0.33$; $P < 0.000001$ for all tests). However, there was considerable

temporal change in the composition found in both *Typha* removed via fangueo treatments (F and FF), particularly in response to seasonal flooding; there was a significant difference between the wet and dry-season communities (Fig. 6; Tables 3 and 4; MRPP, dry 2007 vs. wet 2007, $A = 0.06$, $P < 0.00001$; wet 2007 vs. dry 2008, $P < 0.05$, $P < 0.00001$). In the second dry season, the composition in these plots (F and FF) showed more plot-level variation than in the first year; whereas some of the plots were dominated by *Hymenachne amplexicaulis*, *Cyperus articulatus*, and *Paspalum vaginatum*, others were dominated by *Typha* (compare the locations of the \times symbols in Fig. 6 with the species centroids). As expected, the *Typha*-control plots were strongly dominated by *Typha* and few other species were present in abundance in these plots (Fig. 6; Tables 3 and 4). After *Typha* removal, plots retained little vegetation cover until the start of the first wet season, when the free-floating and floating-rooted species *Neptunia natans* and *Nymphaea amazonum* became dominant. Several emergent species (e.g., *Hymenachne amplexicaulis*, *Paspalum vaginatum*, *Typha domingensis*) also became established during this period but were not dominant due to their small size. During the second dry season in these *Typha*-removed plots, several grass species (e.g., *Hymenachne amplexicaulis* and *Paspalum vaginatum*) and *Typha* all increased in importance (i.e., their importance values increased).

DISCUSSION

Regime shifts often produce ecosystems with properties that enhance stability and resilience; as a result, ecosystem management after a regime shift is challenging and often entails the development of innovative approaches (Suding et al. 2004, Seastedt et al. 2008, Hobbs et al. 2009). Our results quantify the impact of an approach that has been used to manage a landscape-scale *Typha* invasion in Palo Verde National Park (Costa Rica). The approach employed a form of repeated mechanical disturbance (i.e., fangueo) in combination with seasonal flooding and drought to restrict cattail expansion, create habitat heterogeneity, and maintain plant diversity.

Typha resistance and resilience: implications for restoration after a regime shift

Long-term removal of *Typha* is complicated by the combination of r - and K -type strategies that enable *Typha* to be such a dominant, ubiquitous, resistant, and resilient genus (McNaughton 1966, 1975). Established *Typha* stands are highly resistant to management, and resource managers at Palo Verde Marsh experimented with various approaches (e.g., fire, manual cutting, cattle grazing) before selecting fangueo (McCoy and Rodriguez 1994). We expected that management via fangueo would rapidly reduce *Typha* dominance in the first year. Indeed, the fangueo treatment resulted in an immediate and large reduction in *Typha* aboveground

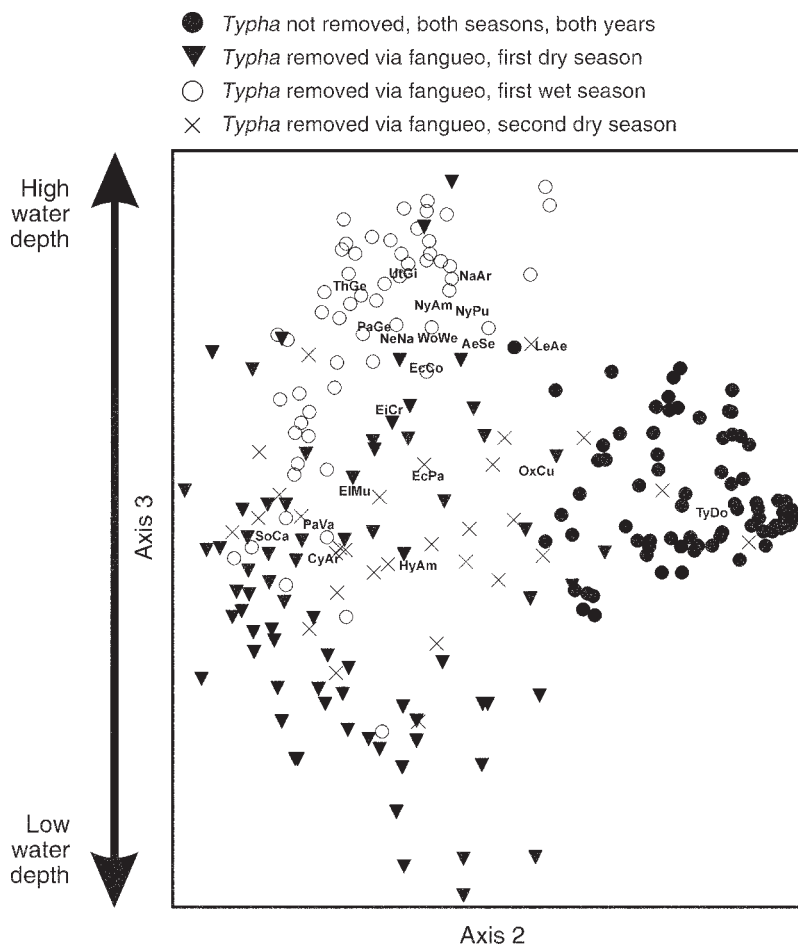


FIG. 6. Impact of *Typha* removal via fangueo and seasonal flooding on plant community composition. This is a nonmetric multidimensional scaling (NMS) ordination of individual plots in species space. Whereas the individual plot treatments are denoted by symbols, the species centroids are denoted by four-letter species codes (see Table 4). Water depth (the only environmental variable we measured with a strong correlation to ordination space) was most strongly correlated to the vertical axis.

biomass, ramet density, and ramet height. Yet we also expected that the landscape-scale expansion and establishment of monotypic *Typha* had enhanced cattail resilience and, that despite effective removal of cattail

via fangueo in the first year, cattail would regenerate and become dominant again without repeated management. Our results indicate that *Typha* stands in Palo Verde Marsh are highly resistant and resilient due to tremen-

TABLE 3. Common plant species in the control and *Typha*-removed via fangueo plots during the dry and wet seasons.

<i>Typha</i> not removed	<i>Typha</i> removed via fangueo		
Both seasons, both years	Dry season 2007	Wet season 2007	Dry season 2008
<i>Typha domingensis</i> (82, 89*)	<i>Paspalum vaginatum</i> (2, 12)	<i>Neptunia natans</i> (20, 65*)	<i>Hymenachne amplexicaulis</i> (13, 44*)
<i>Hymenachne amplexicaulis</i> (1, 6)	<i>Hymenachne amplexicaulis</i> (2, 8)	<i>Nymphaea amazonum</i> (11, 72*)	<i>Neptunia natans</i> (6, 21)
<i>Neptunia natans</i> (1, 3)	<i>Solanum campechiense</i> (1, 46*)	<i>Utricularia gibba</i> (3, 44*)	<i>Typha domingensis</i> (6, 7)
<i>Nymphaea amazonum</i> (1, 4)	<i>Neptunia natans</i> (1, 4)	<i>Hymenachne amplexicaulis</i> (3, 14)	<i>Paspalum vaginatum</i> (4, 18*)
<i>Echinodorus paniculatus</i> (0, 5)	<i>Cyperus articulatus</i> (1, 13)	<i>Paspalum vaginatum</i> (2, 11)	<i>Eichhornia crossipes</i> (3, 21*)

Notes: The five plant species with the highest importance values are shown for each of the four groups illustrated in the nonmetric multidimensional scaling (NMS) analysis (Fig. 6). Species are listed in descending rank order of importance value. The values in parentheses represent the importance value [(mean percentage cover × frequency)/100] and indicator value (percentage of perfect indication for that group; calculated using indicator species analysis, INSPAN) for each species, respectively.

* Indicator values significant at $P < 0.05$.

TABLE 4. Common plant species observed in Palo Verde Marsh during the course of this study.

Species	Code	Life form	Species	Code	Life form
<i>Aeschynomene sensitiva</i>	AeSe	E	<i>Nymphaea amazonum</i>	NyAm	FR
<i>Cyperus articulatus</i>	CyAr	E	<i>Nymphaea pulchella</i>	NyPu	FR
<i>Echinochloa colona</i>	EeCo	E	<i>Oxycaryum cubense</i>	OxCu	E
<i>Echinodorus paniculatus</i>	EcPa	E	<i>Paspalum vaginatum</i>	PaVa	E
<i>Eichhornia crassipes</i>	EiCr	FF	<i>Paspalidium geminatum</i>	PaGe	E
<i>Eleocharis mutata</i>	ElMu	E	<i>Solanum campechiense</i>	SoCa	E
<i>Hymenachne amplexicaulis</i>	HyAm	E	<i>Thalia geniculata</i>	ThGe	E
<i>Lemna aequinoctialis</i>	LeAe	FF	<i>Typha domingensis</i>	TyDo	E
<i>Najas arguta</i>	NaAr	S	<i>Utricularia gibba</i>	UtGi	S
<i>Neptunia natans</i>	NeNa	FF	<i>Wolffia welwitschii</i>	WoWe	FF

Notes: Each species is accompanied by a four-letter code that can be used to interpret the species centroids in the NMS ordination (Fig. 6). Common species were defined as those present in >5% of the plots. The life form abbreviations indicate the species' predominant life form, as follows: E, emergent; FF, free-floating; FR, floating-rooted; and S, submerged.

dous growth and reproduction (both sexual and asexual) at various life history stages. First, *Typha* clonal expansion is rapid; the average rate of vegetative expansion of a mature *Typha* stand into managed areas was about 2.5 m/yr, indicating that established and clonally integrated *Typha* ramets are resistant to management activities and disturbances that do not lead to mortality. Second, the propagule pressure in these areas is great due to: (A) a large *Typha* seed bank; and (B) a large influx of wind-transported seeds from adjacent *Typha* stands. *Typha* germination and establishment rates from these propagules were high. As a result, *Typha* had recruited into most of the managed plots during the two years of our study. Although these seedlings grew faster than most other species, they were not yet clonally integrated, which means that their growth was slow relative to adult *Typha*. At the end of this study, *Typha* dominance in managed areas was still small relative to control areas. Yet we expect that once the seedlings produce new ramets and become clonally integrated, *Typha* will dominate these plots again without additional management (i.e., within 2–4 years). Currently, management via fangueo at Palo Verde Marsh is relatively cheap (\$40/ha in this site) and rapid (one tractor can remove 10–16 ha of *Typha* per day); hence, it has been repeated on an annual basis, which has limited subsequent *Typha* dominance and maintained diversity.

Typha resistance to management is highly dependent upon phenology and hydrology-induced physiological stress (Linde et al. 1976, Apfelbaum 1985). At Palo Verde Marsh, fangueo has recently been implemented in the beginning to middle of the dry season, when the water level is typically <75 cm in depth and receding. Since fruiting at Palo Verde Marsh occurs primarily in the dry season, we expect that *Typha* energy reserves should be lowest during this period. *Typha* store large carbohydrate energy reserves in rhizomes to produce new ramets and recover from disturbance (Linde et al. 1976). Linde et al. (1976) demonstrated the importance of planning management efforts for periods when these energy reserves are at their minimum. In addition to phenology, hydrology plays an important role during

Typha management (Apfelbaum 1985, Sojda and Solberg 1993). Wetland hydroperiod determines plant community composition and can greatly influence the dominance and resistance of cattail and other invasive wetland plants (Zedler and Kercher 2004). From a management perspective, flooding regimes can be utilized to produce anaerobic conditions and physiological stress that can decrease resistance to management (e.g., Sojda and Solberg 1993, Jenkins et al. 2008). In Palo Verde Marsh, ramets that are crushed via fangueo in the beginning of the dry season are subjected to anaerobic stress immediately after fangueo. Shortly thereafter, the water levels recede completely and any ramets that are still alive are subjected to additional physiological stress associated with drought-like conditions. Rapid flooding at the start of the rainy season due to extreme storm events can also lead to *Typha* mortality when young ramets are submerged and subjected to anaerobic conditions.

Diversity maintained by disturbance, propagule bank, and seasonal climate

The biotic assemblages present in tropical, seasonally flooded wetlands like Palo Verde Marsh are defined by a combination of multiple and frequent disturbances (e.g., fire, grazing) and distinct and extreme seasonal climate cycles (i.e., flooding, drought) (Middleton 1999). Community resilience in these dynamic ecosystems is dependent upon a propagule bank that enables rapid post-disturbance recovery (van der Valk 1981, Brock et al. 2003), and disturbance is often responsible for maintaining diversity (Kirkman and Sharitz 1994, Middleton 1999). Our results indicate that, after *Typha* removal, the abiotic filters associated with seasonal flooding and drawdown played an important role in determining plant community change and produced distinct dry and wet-season plant assemblages (Table 3; Fig. 6). During the wet season, the managed plots contained a heterogeneous mixture of plant life forms (e.g., free-floating, floating-rooted, submerged, and emergent). As the water level declined throughout the dry season, the free-floating and floating-rooted species became less abundant. The propagule bank at Palo

Verde Marsh was relatively large and diverse, which enabled post-disturbance regeneration and a rapid increase in plant diversity after *Typha* management via fangueo.

In addition to plant diversity, avian diversity at Palo Verde Marsh has been shown to rapidly increase in response to *Typha* management via fangueo (see McCoy and Rodriguez 1994, Trama 2005). Restoring avian diversity has continuously been one of the primary objectives associated with the various management efforts to restrict *Typha* expansion at Palo Verde Marsh. We conducted an avian survey in a subset of our experimental treatments in order to coarsely gauge the short-term and immediate avian response. These surveys indicated a 98- and 5-fold increase in avian density and richness, respectively, in response to *Typha* management via fangueo (M. J. Osland, *personal observation*).

Based upon our results and the literature, we present a conceptual model that illustrates the role of repeated disturbance (i.e., fangueo) and seasonal hydrologic fluctuations for reducing *Typha* dominance and increasing plant and avian diversity at Palo Verde Marsh (Fig. 7; adapted from successional models developed for temperate and tropical marshes [van der Valk 1981, Middleton 1999]). Without disturbance, *Typha* dominance rapidly increases and plant and avian diversity decrease due to competitive exclusion and reduced habitat heterogeneity, respectively. Repeated disturbances (e.g., fangueo) and seasonal hydrologic fluctuations (e.g., flooding and drawdown) reduce *Typha* dominance and enable plant recruitment from the propagule bank, which results in greater habitat heterogeneity and plant and avian diversity. We suggest that this model is likely applicable to various tropical dry wetlands across the globe where the historical disturbance regime has been altered and monotypic clonal plant invasions have occurred.

Heavy machinery use during restoration: potential impacts on soil properties and seedling emergence

The use of heavy machinery during restoration can be detrimental to soil properties and soil-regulated biotic processes (Lowery and Schuler 1991, Kozlowski 1999). Fangueo is a form of mechanical disturbance that at Palo Verde Marsh entails the use of a tractor. Hence, we hypothesized that fangueo would result in compaction (i.e., higher soil bulk densities relative to areas that did not receive the fangueo treatment). We also expected that the mechanical disturbance associated with fangueo would have an impact on the seed bank and alter the pool of plant species that germinate from the seed bank. However, we found no apparent short-term impact of fangueo on soil bulk density or seed bank germinant composition. Importantly, fangueo had no short-term impact on any of the soil properties we measured. The soil bulk density in Palo Verde Marsh is relatively high compared to many other wetlands, particularly wetlands

with highly organic soils and low soil bulk densities. Tractor use in wetlands with low soil bulk densities is not advised, because it would likely result in long-lasting physical and ecological change, and also probably be risky for tractor operators due to high soil instability. We note that we were not able to measure plant available inorganic nitrogen, which is often elevated after disturbances that remove plant biomass (Schlesinger 1997, Richardson 2008b). We also stress that our soil analyses assess the short-term impact of the mechanical disturbance and not the long-term impact of *Typha* removal.

Linkages between nutrient inputs and landscape-scale Typha expansion

In many tropical and subtropical wetlands, elevated phosphorus (P) inputs have been linked to landscape-scale *Typha* expansions (Craft and Richardson 1997, Johnson and Rejmánková 2005, Hagerthey et al. 2008). *Typha* dominance is unlikely in wetlands with low P availability and high N:P ratios (Richardson et al. 1999, Debusk et al. 2001, Craft and Richardson 2008). Most published biogeochemical investigations in Central American wetlands have been conducted in the uniquely oligotrophic, calcareous, and P-limited wetlands of the Yucatan Peninsula (Rejmánková et al. 1996, Rejmánková 2001) and a P-limited coastal mire in Panama (Troxler 2007). The results from these studies and the Everglades region of Florida (Davis 1994, Richardson et al. 1999, Noe et al. 2001) are occasionally extrapolated to all wetlands in the region to imply that most Central American wetlands may be P limited. However, the low soil N:P ratios (mean \pm SE = 6.9 ± 0.5) found here indicate that Palo Verde Marsh and other wetlands in the region may be N-limited. *Typha* foliar N:P measurements from another wetland in PVNP (La Bocana Marsh) are also indicative of nitrogen limitation (7.6 ± 0.2 ; mean \pm SE) (see the following for discussion of wetland N:P ratios and nutrient limitation: Koerselman and Meuleman 1996, Verhoeven et al. 1996, Bedford et al. 1999, Güsewell et al. 2003). The nutrient-induced expansion of *Typha* in the Everglades region may be the most infamous and extensively studied regime shift that has occurred in freshwater wetland ecosystems (see Gunderson 2001, Hagerthey et al. 2008, Richardson 2008b). As a result, specific soil eutrophication thresholds have been identified and have been used to elucidate landscape-scale plant community transformations. We note that, on a volume basis, the mean soil P concentration at Palo Verde Marsh ($530 \mu\text{g P/cm}^3$) is far above the identified threshold for *Typha* invasion in the Everglades, which is $\sim 50 \mu\text{g P/cm}^3$ [calculated using a bulk density of 0.1 g/cm^3 (Craft and Richardson 2008) and a mass-basis threshold of 500 mg P/kg (Richardson et al. 1999, Debusk et al. 2001, Craft and Richardson 2008, Hagerthey et al. 2008)]. These comparisons are important because they characterize the potential for *Typha*

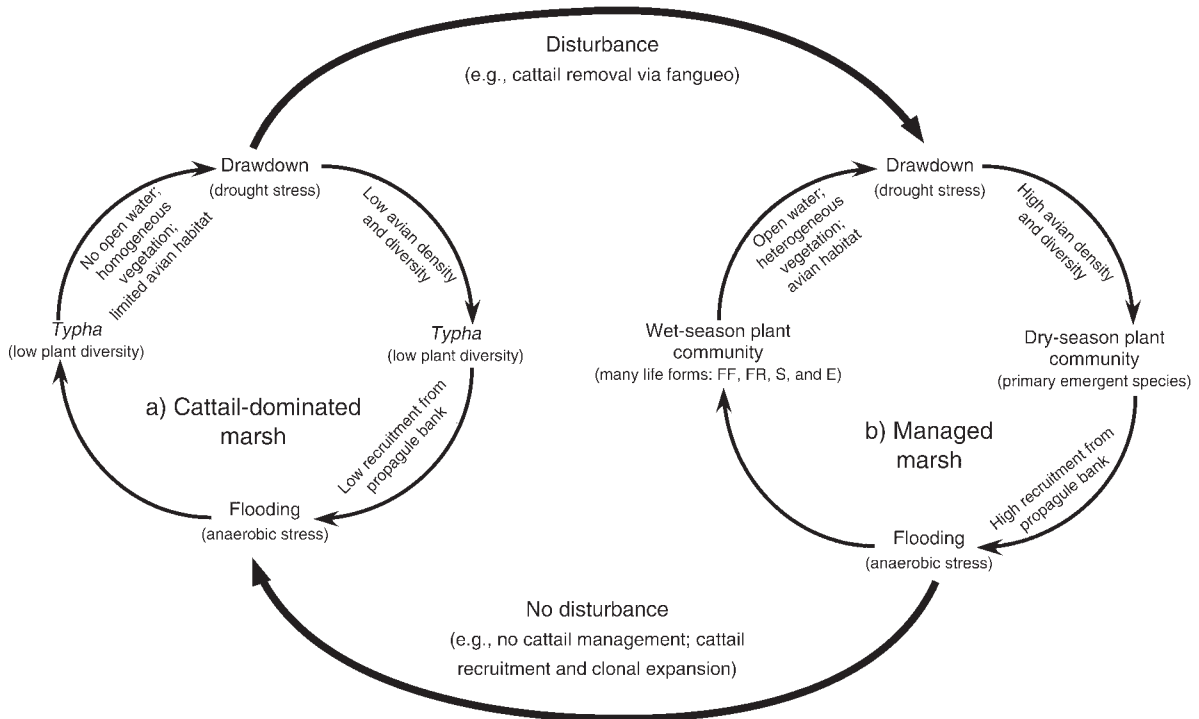


FIG. 7. A conceptual model illustrating the role of repeated disturbance and seasonality for maintaining diversity at Palo Verde Marsh (adapted from van der Valk [1981] and Middleton [1999]). The model includes two marsh categories: (a) the highly resistant *Typha*-dominated marsh and (b) the seasonal and heterogeneous managed marsh. Note that the managed marsh is not a steady state; after 2–4 years without disturbance, high *Typha* recruitment and clonal expansion will lead to *Typha* dominance. Frequent disturbances (e.g., repeated fangueo, grazing, flooding) are required to limit *Typha* dominance, create space for plant recruitment from the propagule bank, and maintain the seasonal plant and avian communities found in the managed marsh. Plant life form abbreviations are: FF, free-floating; FR, floating-rooted; S, submerged; E, emergent.

dominance in Palo Verde Marsh and highlight the distinct biogeochemical differences between tropical dry wetlands like Palo Verde Marsh and the P-limited tropical peatlands that have been studied in the Everglades, the Caribbean coast of Belize, and the Caribbean coast of Panama.

Summary

In wetlands across the globe, anthropogenically induced regime shifts in the form of clonal plant invasions (e.g., *Typha*, *Phragmites*, *Phalaris*) are becoming increasingly common and have resulted in diversity loss and altered wetland conditions (Zedler and Kercher 2004, Hagerthey et al. 2008). Since the monodominant ecosystems that are produced during such transformations are often highly resistant to management and restorative efforts, there has been much interest in approaches that can be used to reduce the dominance of these species and maintain diversity. In this study, we quantified the impact of an approach that has been used at a local scale in northwestern Costa Rica to increase wetland diversity after a rapid landscape-scale *Typha* expansion. The approach uses a novel form of disturbance (i.e., fangueo) in combination with seasonal

hydrology to reduce resistance to management, create habitat heterogeneity, and maintain diversity.

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