

DOES HARVESTING SUSTAIN PLANT DIVERSITY IN CENTRAL MEXICAN WETLANDS?

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Abstract: In Central México, wetland plants are harvested for weaving, fodder, and fertilizer. To test whether harvesting alters plant diversity, we compared the effects of harvesting all vegetation once, follow-up harvesting of *Typha domingensis* Pers. one or three more times, and a non-harvested control, using two sites differing in water depth in an annually burned wetland near Morelia, México. After one year, harvesting treatments increased species richness at both the plot (14-m²) and wetland scales, increased the Shannon diversity index at the plot and subplot (1-m²) scales, and changed plant community composition (measured by Bray-Curtis distance) relative to control plots. Response among harvesting treatments was similar, and increased *Typha* harvesting did not have additive effects on *Typha* or on community composition. Grasses and short forbs (< 0.5-m tall) significantly increased in importance value in harvested plots, as did five individual forb species that were capable of vegetative spread. Uncommon species were significantly more likely to be found only in harvested plots than only in control plots, and new species (not initially present at the site) tended to recruit in harvested plots. Most new species were perennials that could likely tolerate additional harvesting. All harvesting treatments reduced *Typha* height, density, and rhizome starch reserves after five months, and responses were significantly affected by site, water depth, flowering ramet density, and pre-treatment values. *Typha* recovered in all harvested plots after one year, even when harvested four times, although flowering-ramet density declined in the wetter site. Community composition was more highly correlated with water depth and litter cover than with harvesting in an NMS ordination including both sites. Within sites, harvesting, light availability, leaf area index, and litter cover correlated similarly with variation in community composition. Given that our treatments reflect a subset of actual local management practices, harvesting could provide a sustainable and economically attractive management strategy for biodiversity conservation in this system, while the cessation of harvesting could lead to species loss.

Key Words: dominance, haying, Mexico, non-timber forest products, species richness, *Typha domingensis*, wetland management

INTRODUCTION

European ecologists have shown that harvesting vegetation can create and maintain novel community types (Godwin 1941) and that cutting and removing plants generally increases species richness relative to unmanaged plots in a variety of human-modified wetland and upland systems (e.g., Wheeler and Giller 1982, Bakker 1989, Kull and Zobel 1991, Peet et al. 1999, Hansson and Fogelfors 2000). Theory predicts that in productive environments,

harvesting reduces competition by dominant species that would otherwise lead to the exclusion of subordinates (Grime 1973). Harvesting removes leaf biomass at a uniform height, which decreases the asymmetry of light competition between tall and short species (Zobel 1992) and increases light penetration to the soil surface, creating regeneration niches (Grubb 1977) for species with life history strategies adapted to or tolerant of the management regime (Naveh and Whittaker 1979, Denslow 1980, Peet et al. 1983).

Despite the widespread use of harvesting in Europe, conservation managers in North America more often use prescribed fires to maintain diversity (Collins *et al.* 1998), especially in wetlands (Bedford *et al.* 1999, Middleton *et al.* 2006). In some systems, wetland scientists assume a categorically negative correlation between human “disturbance” (including mowing) and “ecological condition” (e.g., Wardrop *et al.* 2007). While fire alone could reduce dominance and litter accumulation enough to allow the persistence of short-statured or less-competitive species (Leach and Givnish 1996), maintaining diversity in productive landscapes might also require the removal of biomass through grazing or harvesting (Collins *et al.* 1998).

Highly productive North American wetlands with an extensive cultural history of harvesting and burning include those of Mexico’s central altiplano region, where people have harvested wetland plants for millennia. *Typha* spp. (cattail) and *Schoenoplectus* spp. (bulrush) have been used for weaving by multiple cultural groups including the P’urépecha or Tarascan (Reyes 1992) and the Mexica or Aztec (Heyden 1983). These plants were also harvested to fertilize and construct fields in chinampas wetland agricultural systems, and at least since the Spanish conquest, for animal fodder (West 1948, Heyden 1983, Albores Zárate 1995). *Typha domingensis* Pers. (hereafter *Typha*) and *Schoenoplectus* spp. are currently harvested extensively in parts of this region, predominantly for use in woven craft products, or artesanías (Reyes 1992). *Typha* can form nearly monotypic stands throughout its wide sub-tropical and tropical range (Lot and Novelo 1988, Urban *et al.* 1993, McCoy *et al.* 1994), as can *Schoenoplectus* spp. (Rojas Moreno and Retana 1995, Kandus and Malvárez 2004). It is not clear, however, if the subordinate plants in these systems simply tolerate historical harvesting regimes, or if they require harvesting to avoid competitive exclusion, even when annual fires remove accumulated litter.

Whether we consider harvesting an unusual perturbation or a characteristic event depends on the scale of observation we impose and the context we acknowledge (Allen and Starr 1982). Here, we ask if diversity increases with harvesting in wetlands that have long experienced such management. We hypothesized that 1) an initial harvest and follow-up selective harvest of *Typha* would especially reduce *Typha* as well as the co-dominant *Schoenoplectus americanus* (Pers.) Volkart ex Schinz & Keller (hereafter *Schoenoplectus*); 2) sub-dominant species would increase in cover and frequency under harvesting; and 3) species not present in extant

vegetation would recruit from the seed-bank under harvesting treatments. We compared four treatments: one-time harvesting (cutting and removing all plants), follow-up selective harvesting of *Typha* either one or three more times, and no manipulation, at a protected-area wetland in Central Mexico that burns annually. We assessed vegetation responses as leaf area index (LAI), light interception, and cover by species, plus height, ramet density, and flowering of *Typha*, and height of *Schoenoplectus*. We expected diversity to increase after harvesting and all measures of *Typha* to decrease temporarily, and we predicted that plots with many flowering *Typha* ramets would show reduced re-growth after harvesting (Grace and Wetzel 1982). We also assessed starch depletion, because *Typha latifolia* L. uses high concentrations of starch stored in the rhizome central core for future above-ground growth (Kausch *et al.* 1981). We evaluated our results in light of actual harvesting practices in this region in order to evaluate the potential importance of plant harvesting for biodiversity conservation.

METHODS

Site Description

We conducted field experiments at the 10-ha Mintzita wetland in Morelia, Michoacán, México (19°38'25" N, 101°16'25" W, 1940 m). Historically, parts of Mintzita were harvested and grazed, but due to recent protected-area status (A. Peláez, Municipio de Morelia, personal communication), harvesting and grazing have been minimal, at least since 2002. In four of the last five years, and probably historically as well, nearby agricultural fires escaped and burned Mintzita in February, after leaves senesced. Maize fields and sub-tropical matorral scrub, used for cattle grazing, surround the wetland. Although Mintzita is fed by ground water year round, highly seasonal precipitation (800 mm from June to September, Instituto Nacional de Estadística, www.inegi.gob.mx/est/contenidos/espanol/rutinas/ept.asp?t=mamb98&c=5843, accessed May 2007) can raise water levels 5–10 cm during the summer (S. Hall, unpublished data). Water in the main spring is base-rich, averaging 26 mg/l Ca and 40 mg/l Mg, with pH 7.5 (Figuroa-Amparo 2001). Heavy detergent use in the main spring has recently increased phosphorus loads (R. Lindig-Cisneros, unpublished data).

The main springs at Mintzita produce about 1,700 l/s and supply 30%–40% of the water for Morelia, a city of over 500,000 (A. Peláez, Municipio de Morelia, personal communication). The

spring and associated stream also provide habitat for several endangered endemic species of fish (Soto-Galera et al. 1999), and similar wetlands in nearby Zacápu, Michoacán could qualify as Ramsar Wetlands of International Importance because of their abundance and diversity of waterfowl (Pérez-Arteaga et al. 2002). However, the flora of these wetlands is poorly studied. *Typha domingensis* (chuspata, cattail) and *Schoenoplectus americanus* (espadaña, three-square bulrush) dominate the emergent plant community. *Schoenoplectus* frequently dominates in areas without standing water during the dry season, whereas dominance shifts to *Typha* with increasing water depth (R. Lindig-Cisneros, unpublished data). *Salix* sp. (willow), *Acacia* spp. (huisache), and *Opuntia* spp. (prickly-pear) dominate adjacent uplands.

Experimental Design

We chose drier and wetter sites within Mintzita to test the robustness of our treatment response across an environmental gradient at the site (Keddy 1990). The drier site had water near or below the soil surface in 2006 and 2007, while the wetter site always had standing water and was 5 cm deeper on average. Neither site had been harvested or grazed for at least five years. We randomly assigned four replicates of each of three harvesting treatments and an un-manipulated control to 16 contiguous 7 m × 2 m plots at each site. Plots were sized so that each would contain a gradient of dominance from *Typha* to *Schoenoplectus* along the 7-m axis, and to mimic a shape and area that people have been observed to harvest in one day using local methods (S. Hall, unpublished data). Treatments were: 1) harvest all above-ground vegetation at 20 cm above the soil surface; 2) harvest as in treatment 1 and then selectively harvest all *Typha* shoots once after the tallest ramets at our sites had regrown to 1.6 m (half the average pre-cut height of *Typha*); 3) harvest as in treatment 1 and then selectively harvest *Typha* shoots three times after re-growth to 1.6 m; and 4) control (no harvest). Local harvesters normally use a machete or long-handled sickle, but we used a gas-powered brush-saw (EFCO 8250, www.emak.it) for the initial harvest treatment (May 2006) in order to cut all plots at both sites and remove cut vegetation by hand on the same day. Our brush-saw cuts were qualitatively similar to those of traditional methods. After the initial harvest, we selectively harvested *Typha* regrowth in July (treatment 2), or July, August, and October (treatment 3), using machetes, while avoiding other plant species. Local people often harvest in May before the rainy season, when

standing crop is near maximum and when dry conditions prevent drying leaves from molding. Some people continue to harvest throughout the rainy season, harvesting the same plants up to four times a year (S. Hall, unpublished data). Similar to our treatments, most local harvesters consciously cut *Typha* above the water surface, or between 20–50 cm above the soil surface.

Data Collection

We positioned four 1-m² subplots uniformly along the 7-m plot axis of each plot. Each subplot had a 0.5-m buffer between the adjoining subplot and the plot boundary. In these subplots, we recorded 1) percent cover of plant species using a modified Braun-Blanquet (1932) scale (0, < 1, 1–5, 6–25, 26–50, 51–75, and 76–100%), 2) presence of flowers, *Typha* flowering and non-flowering ramet density, and 3) height of the three tallest *Typha* and *Schoenoplectus* ramets in the entire subplot. We recorded all of the above data in May 2006 before treatment application, and then post-treatment in August 2006 and May 2007. *Typha* height, density, and water depth were also recorded at the time of subsequent harvesting treatments and two weeks after each harvesting in July, August, and October. In plots assigned to harvesting treatments, ramet regrowth was classified as “re-sprout” if tissue emerged from a cut ramet surface or “new growth” if from a new rhizome bud. In plots assigned to treatments 2 and 3, *Typha* re-growth was collected by subplot and dried at 60°C to constant weight for biomass determination. Plant species identifications were corroborated using herbaria at the University of Michoacán (UMSNH, herbarium code EBUM) and Pátzcuaro Institute of Ecology (IEB). Nomenclature followed McVaugh (1984), Rzedowski and Rzedowski (2001), and the USDA plants database (<http://plants.usda.gov>, accessed 8/1/07).

We also recorded water depth at the center of each subplot, and averaged depths from July and August in each subplot (when all plots were inundated) to create an index of relative water depth to use as a co-variate in linear models. In May 2007, we measured the percentage of ambient solar radiation not absorbed by the canopy (τ) and leaf area index (LAI) using a ceptometer (Accu-Par LP-80, Decagon Devices Inc., Pullman, WA). Because the canopy had two distinct strata (the upper formed by *Typha* and *Schoenoplectus*, the lower by forbs, grasses, and other graminoids), we measured τ and LAI at ground level immediately above accumulated litter, as well as immediately above the sub-canopy vegetation (typically at 1 m above the ground). The

86.5-cm ceptometer wand had 80 separate sensors, each of which we averaged over five separate measurements at 20-cm intervals within each subplot to account for intra-subplot variation. To test if harvesting increased light levels in non-harvested plots because of edge effects, we measured τ in July 2007 after implementing a separate harvesting experiment in a subset of plots; non-harvested plots did not differ in τ when either one or both neighboring plots were harvested (ANOVA, $F_{2,14} = 0.8$, $p = 0.48$).

Rhizome Analysis

We harvested *Typha* rhizomes in October 2006 (five months after the initial cut) from a subset of experimental plots to measure rhizome starch concentrations. At this time, rhizome starch concentrations were likely at their peak because ramets were mostly senesced and carbohydrates recovered from leaves (Linde *et al.* 1976). From each of two replicate plots of each treatment in each site, we selected the most vigorous (tallest and greenest) ramets outside of the 1-m² subplots. We observed that after harvesting, ramets could either re-sprout from the original cut ramet surface, or that new ramets (produced from rhizome buds) could emerge from the soil; we sampled rhizomes below re-sprouting ramets because these would likely have greater reserves. We excavated rhizomes by making a vertical circular cut with a machete through the soil around the base of the ramet. To achieve uniform rhizome samples, we trimmed rhizomes just above the upper-most vegetative bud (approximately at the shoot base) and below the lowest vegetative bud (normally where the rhizome begins to curve horizontally). We dried the rhizomes to constant weight (2–3 days) at 75°C and stored them at –10°C before analyzing starch concentrations colorimetrically (Hassid and Neufeld 1964) and converting concentrations to total starch mass per rhizome sample.

Statistical Analysis

We averaged *Typha* height and density in subplots within plots (to avoid pseudo-replication) for the response variables in linear models, with treatment and site as factor variables, including interactions. To account for effects of environmental variation between plots, we included three continuous variables: relative water depth (described above), the pre-treatment value of each response variable, and the percentage of *Typha* ramets in flower. We used rhizome starch mass, LAI, and percent light

infiltration (τ) as the response variables in models that included treatment, site, and relative water depth as predictors.

We measured species richness and Shannon's diversity index at the subplot (again averaging subplots within plots), plot, and total wetland scales for each treatment. Linear models for these response variables included treatment and site as factor variables, and pre-treatment richness, water depth, and τ as potential continuous variables. We generated all of the previous linear models using R Version 2.4.1 (R Foundation for Statistical Computing, 2006), and used the Tukey HSD correction for multiple comparisons. We chose a priori to make pairwise contrasts between control plots and harvested plots even in the absence of significant global treatment effects in ANOVA. At the total wetland scale, we used subplot-based species rarefaction curves and 95% confidence intervals generated in EstimateS Version 8 (R. Colwell, University of Connecticut, 2006) to compare species richness between treatments.

To test for treatment effects on community composition, we performed ANOSIM (analysis of similarities), a test comparing rank multivariate similarities of plots within and among treatments (Clarke and Warwick 2001), using a Bray-Curtis distance matrix of species cover class data and the "vegan" package (Version 1.8) in R. We compared correlations of treatments with species importance value, presence of flowers by species, and plant functional groups using indicator species analysis (Dufrene and Legendre 1997) as implemented in PC-ORD 5.08 (MjM Software, Gleneden Beach, OR). This test compares observed versus expected importance values (using species frequency and abundance) with a Monte-Carlo randomization of treatment identity. We used grasses, non-grass graminoids, shorter forbs (< 0.5-m tall, chosen to reflect the upper boundary of a group of forbs with similar heights), taller forbs (> 0.5-m tall), forbs combined, and woody plants as functional groups. We used $\alpha = 0.10$ for indicator species analysis because of the low frequency of most species. We generated a Non-Metric Scaling (NMS) ordination of May 2007 cover class data using a Bray-Curtis distance matrix to qualitatively examine correlations between treatments and environmental factors with axes of variation.

RESULTS

In total, we found 44 species in our plots over the three sample periods; 27 were perennials, 14 were annual or short-lived perennials, and three were

Table 1. Species list with life history characteristics and treatment correlation. We defined vegetative spread to include species with rhizomes, stolons, or that rooted from leaf nodes. New recruits were recorded in August 2006 (indicated by "August") and in May 2007 (indicated by "May"). Italicized entries in the "New recruit" column represent species that appeared to be new recruits in the month shown, but that might actually have been present earlier and combined with morphologically similar species. Treatment and site correlations were measured using indicator species analysis for either harvested plots combined or control plots; correlations with $p < 0.10$ were listed, with an additional *, **, or *** for $p < 0.05$, $p < 0.01$, and $p < 0.001$, respectively. "Unique" species were found only in one treatment (although potentially in multiple plots).

Species and authority	Life span	Growth form/origin	Vegetative spread	New recruit	Treatment correlation in May 2007	Site correlation in May 2007	Treatment in which species was unique in May 2006	Treatment in which species was unique in Aug. 2006	Treatment in which species was unique in May 2007
<i>Acmella oppositifolia</i> (Lam.) R.K. Jansen var. <i>repens</i> (Walt.) R.K. Jansen	perennial	forb	yes	May	—	wetter	—	—	harvest
<i>Agrostis hyemalis</i> (Walt.) B.S.P.	perennial	grass	no	May	—	—	—	—	harvest
<i>Andropogon glomeratus</i> (Walt.) B.S.P.	perennial	grass	—	May	harvest	—	—	—	harvest
<i>Arenaria paludicola</i> Robins	perennial	forb	yes	—	—	—	—	—	—
<i>Berula erecta</i> (Huds.) Coville	perennial	forb	yes	—	harvest **	—	—	—	—
<i>Bidens laevis</i> (L.) B.S.P.	either	forb	no	—	harvest *	wetter ***	—	—	—
<i>Carex comosa</i> Boott	perennial	graminoid	yes	May	—	—	—	—	harvest
<i>Cyperus niger</i> Ruiz & Pavón	either	graminoid	yes	August	—	—	—	harvest	harvest
<i>Rhynchospora</i> sp.	perennial	graminoid	—	August	—	—	—	harvest	—
<i>Drymaria villosa</i> Cham. & Schlecht.	either	short forb	no	May	—	—	—	—	harvest
<i>Eclipta prostrata</i> (L.) L.	either	short forb	yes	August	—	—	—	harvest	harvest
<i>Eleocharis rostellata</i> (Torr.) Torr.	perennial	graminoid	yes	—	—	drier ***	—	—	—
<i>Eleocharis acicularis</i> (L.) Roemer & J.A. Schultes	perennial	graminoid	yes	—	—	—	—	—	harvest
<i>Epilobium ciliatum</i> Raf.	perennial	forb	yes	—	—	drier *	—	—	—
<i>Eupatorium</i> sp.	perennial	forb	yes	—	—	drier **	—	—	—
<i>Fraxinus</i> sp.	perennial	tree	—	May	—	—	—	—	harvest
<i>Galium trifidum</i> L.	perennial	forb	no	—	control **	drier *	—	—	—
<i>Gnaphalium americanum</i> (P. Mill.) Weddell	either	short forb	no	—	—	—	—	—	—
<i>Hydrocotyle verticillata</i> Thunb.	perennial	short forb	—	—	harvest *	drier *	—	—	—
<i>Juncus ebracteatus</i> Liebm.	perennial	graminoid	yes	May	—	—	—	—	harvest
<i>Lactuca scariola</i> L.	either	introduced forb	no	—	—	drier *	—	—	—
<i>Lasiantha aurea</i> (D. Don) Becker	perennial	short forb	no	May	—	—	—	—	harvest
<i>Leersia hexandra</i> Sw.	perennial	grass	yes	—	—	wetter	—	—	—
<i>Ludwigia peploides</i> (Kunth) Raven	perennial	forb	yes	August	—	—	—	harvest	—
<i>Lythrum vulneraria</i> Schrank	perennial	forb	—	—	—	wetter **	harvest	—	—
<i>Mimulus glabratus</i> Kunth	perennial	forb	yes	—	harvest	wetter	—	—	—
<i>Picris echioides</i> L.	either	introduced forb	no	May	—	—	—	—	harvest
<i>Polygonum hydropiperoides</i> Michx.	perennial	forb	yes	—	—	wetter **	—	—	—

Table 1. Continued.

Species and authority	Life span	Growth form/origin	Vegetative spread	New recruit	Treatment correlation in May 2007	Site correlation in May 2007	Treatment in which species was unique in May 2006	Treatment in which species was unique in Aug. 2006	Treatment in which species was unique in May 2007
<i>Polygonum punctatum</i> Ell.	either annual	forb introduced	no	May	—	wetter *	—	—	—
<i>Polygonum monspeliensis</i> (L.) Desf.	annual	grass	yes	August	—	drier **	harvest	harvest	harvest
<i>Polygonum elongatum</i> Kunth	perennial	grass	—	May	—	—	—	—	harvest
<i>Ranunculus petiolaris</i> Kunth ex DC.	perennial	short forb	no	May	—	—	—	—	harvest
<i>Rorippa palustris</i> (L.) Bess.	either	short forb	no	—	—	—	—	—	—
<i>Sagittaria</i> sp.	either	short forb	no	—	—	—	harvest	harvest	harvest
<i>Salix</i> sp.	perennial	shrub	yes	May	—	—	—	—	harvest
<i>Scheuchzeria americanus</i> (Pers.) Volkart ex Schinz & R. Keller	perennial	graminoid	yes	—	—	drier ***	—	—	—
<i>Schoenoplectus californicus</i> (C.A. Mey.) Palla	perennial	graminoid	yes	—	—	wetter *	—	control	—
<i>Solanum americanum</i> P. Mill.	either	forb	no	—	—	drier *	—	harvest	—
<i>Sonchus oleraceus</i> L.	either	introduced forb	no	May	—	—	—	—	harvest
<i>Typha domingensis</i> Pers.	perennial	graminoid	yes	—	—	wetter ***	—	—	—
Poaceae 1	—	grass	—	May	—	—	—	—	harvest
Unknown 1	—	forb	—	May	—	—	—	—	harvest
Unknown 2	—	forb	—	May	—	—	—	—	control

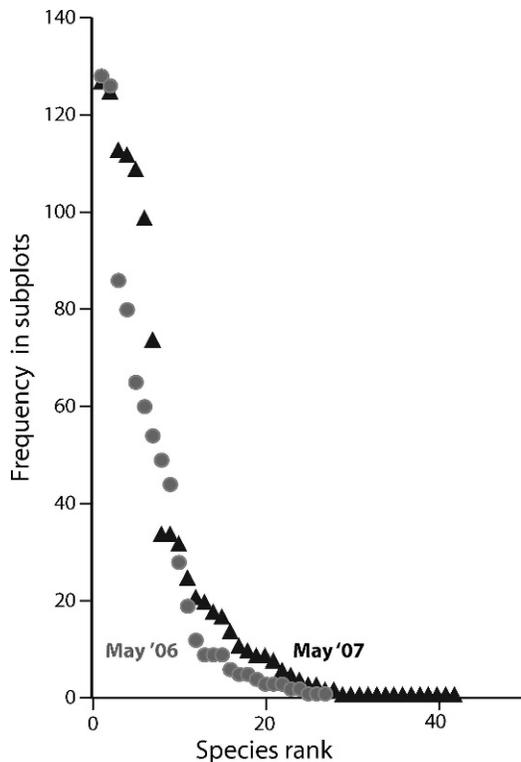


Figure 1. Species rank frequency distribution for both the drier and wetter sites combined in May 2006 (grey circles) and May 2007 (black triangles).

unknowns (Table 1; Rzedowski and Rzedowski 2001). Relative to the initial survey in May 2006, five “new species” recruited in August 2006 and 13 new species recruited in May 2007, excluding four species that might have been lumped in the initial sample (Table 1). All five of the new species in August 2006 occurred only in harvested plots; four of these were annuals. Twelve of the 13 new species in May 2007 were unique to harvested plots, while only one was unique to control plots. At least nine of the new species in May 2007 were perennials, one was annual, and three were unknown. Most species were uncommon at Mintzita (Figure 1, Table 1); 14 of the 44 species were found in only one subplot, and 17 more were found in fewer than 20 of the 128 subplots.

Species Response to Treatments

Before harvesting (May 2006) and three months after the initial harvest (August 2006), total species richness was similar among treatments at the whole plot and subplot scales (ANOVA, $F_{3,26} = 0.5$ and 0.3 , $p = 0.70$ and $p = 0.85$ for the plot and subplot scales in May; $F_{3,26} = 0.3$ and 0.7 , $p = 0.79$ and $p = 0.56$ in August), and the control did not differ from all harvest treatments combined ($T_{28} = 0.23$ and -0.23 , $p = 0.41$ and $p = 0.59$ for the plot and

subplot scales in May; $T_{28} = -0.17$ and 0.56 , $p = 0.57$ and $p = 0.29$ in August). Species rarefaction curves by treatment were similar at the wetland scale (overlapping 95% confidence intervals, not shown; Table 2). However, one year after the initial harvest treatment, species richness and the Shannon diversity index differed by treatment at the plot scale after taking pre-treatment values into account (Table 2), and species richness also differed at the wetland scale (Figure 2). Considering all treatments individually, only the plots harvested four times had greater total richness (31 vs. 22 species, rarefaction curves, Figure 2), mean richness (14.8 vs. 11.0, $p = 0.011$, Tukey correction), and Shannon index (2.32 vs. 2.07, $p = 0.015$, Tukey correction) at the plot scale. Harvest treatments did not differ from each other in pairwise comparisons (Tukey $p > 0.10$), but harvested plots combined had greater richness (13.5 vs. 11 species/plot, $T_{28} = 2.32$, $p = 0.014$) (Figure 2) and Shannon values (2.26 vs. 2.07, $T_{28} = 2.69$, $p = 0.006$) at the plot scale than the control (Table 2). Species richness was similar for the two sites, and both responded similarly to harvesting. Harvested plots at the drier and wetter sites averaged 12.5 and 13.3 species, respectively, compared to 10.5 and 11.5 species in control plots. At the 1-m² subplot scale, harvest treatments combined had similar species richness to the control (Figure 2, 8.6 vs. 7.7 species/m², $T_{28} = 1.52$, $p = 0.07$), but had significantly greater Shannon index (1.99 vs. 1.84, $T_{28} = 2.15$, $p = 0.02$). There were no significant effects when harvesting treatments were considered individually ($F_{3, 26} = 1.6$ and 2.3 , $p = 0.21$ and $p = 0.10$ for richness and Shannon, respectively).

Three months after the initial harvest, both *Typha* ($p = 0.005$) and *Schoenoplectus* ($p = 0.03$) had greater importance values in control treatments according to indicator species analysis, while no other species or functional group had a significant treatment correlation at this time ($p > 0.10$). By May 2007, one year after the initial harvest, three species correlated significantly ($p < 0.05$) with harvested plots, two correlated marginally ($p < 0.10$) with harvested plots, while one species correlated significantly with control plots ($p < 0.05$) (Table 1). Neither *Typha* nor *Schoenoplectus* correlated significantly by May 2007. Flowering versus vegetative status did not significantly correlate with treatments ($p > 0.10$). Grasses and shorter forbs (< 0.5 m, Table 1) showed significant correlations with harvested plots ($p = 0.03$ and $p = 0.02$, respectively), while all forbs combined, graminoids, and woody plants did not ($p > 0.10$). Eighteen species showed a significant site correlation, nine for the wetter site and nine for the drier (Table 1).

Table 2. Species richness and Shannon index by treatment, scale, and sampling date (A), and linear models for species richness (B) and Shannon index (C) at the plot scale for May 2007 data.

A) Species richness and Shannon index values by treatment, scale, and sampling date, \pm SE					
Treatment	Richness (site scale)	Richness (plot scale)	Richness (subplot scale)	Shannon (plot scale)	Shannon (subplot scale)
May 2006					
control	21	9.88 \pm 0.56	6.56 \pm 0.40	1.83 \pm 0.16	1.49 \pm 0.18
1 harvest	21	8.75 \pm 0.42	6.41 \pm 0.33	1.79 \pm 0.13	1.46 \pm 0.17
2 harvest	19	9.00 \pm 0.65	6.44 \pm 0.44	1.82 \pm 0.18	1.47 \pm 0.19
4 harvest	19	9.50 \pm 0.47	6.03 \pm 0.41	1.79 \pm 0.16	1.35 \pm 0.21
August 2006					
control	21	10.38 \pm 0.43	6.50 \pm 0.28	1.98 \pm 0.13	1.67 \pm 0.14
1 harvest	23	11.00 \pm 0.53	6.81 \pm 0.37	2.18 \pm 0.17	1.83 \pm 0.14
2 harvest	23	10.88 \pm 0.49	7.03 \pm 0.34	2.16 \pm 0.17	1.81 \pm 0.16
4 harvest	21	10.38 \pm 0.39	6.66 \pm 0.31	2.12 \pm 0.14	1.77 \pm 0.13
May 2007					
control	22	11.00 \pm 0.55	7.70 \pm 0.39	2.07 \pm 0.15	1.84 \pm 0.15
1 harvest	29	13.40 \pm 0.53	8.30 \pm 0.41	2.24 \pm 0.14	1.97 \pm 0.14
2 harvest	27	12.40 \pm 0.51	8.50 \pm 0.43	2.20 \pm 0.15	1.99 \pm 0.16
4 harvest	31	14.80 \pm 0.53	8.90 \pm 0.37	2.32 \pm 0.11	2.02 \pm 0.13
B) Linear model for species richness at the plot scale in May 2007					
	d.f.	M.S.	F	p-value	
Treatment	3	20.08	3.99	0.02	
Site	1	4.5	0.89	0.35	
Pre-treatment richness	1	5.83	1.16	0.29	
Residuals	26	5.04			
C) Linear model for Shannon diversity index at the plot scale in May 2007					
	d.f.	M.S.	F	p-value	
Treatment	3	0.090	3.77	0.02	
Site	1	0.02	0.67	0.42	
Pre-treatment Shannon	1	0.08	3.38	0.08	
Residuals	26	0.02			

Considering all species in the wetland, in May 2007, 20 species were unique to harvested plots, whereas one species was unique to control plots (Table 1). Harvested plots had significantly more unique species than control plots after accounting for differences in sample size using a chi-square goodness of fit test ($\chi_1 = 4.59$, $p = 0.03$). There was no significant difference in unique species between treatments in May or August 2006 using the same test ($p > 0.10$); before treatment, three species were unique to harvested plots and none was unique to control plots, while in August 2006, eight species were unique to harvested plots whereas one was unique to control plots (Table 1).

Treatment Effects on Community Composition

Community composition (defined here as the Bray-Curtis distance matrix of species cover class

data) differed greatly by site before and after treatment (ANOSIM $R = 0.96, 0.55, 0.64$, all $p < 0.001$, for May 2006, August 2006, and May 2007, respectively), so we analyzed sites individually. Before the initial harvest in May 2006, community composition did not differ by treatment in the drier site ($R = -0.01$, $p = 0.46$) or in the wetter site ($R = -0.13$, $p = 0.92$), nor did it differ after comparing the control and harvested plots combined ($R = 0.05$, $p = 0.31$ for the drier site and $R = -0.12$, $p = 0.88$ for the wetter site). In August 2006 and May 2007, we found no main effects of treatments on community composition ($R = 0.13$, $p = 0.12$ and $R = 0.07$, $p = 0.25$), but we found significant differences between harvested plots combined and control plots in both cases. In August, composition differed between control and harvested plots combined in the drier site ($R = 0.49$, $p = 0.003$), but did not differ significantly in the wetter site ($R = 0.25$, p

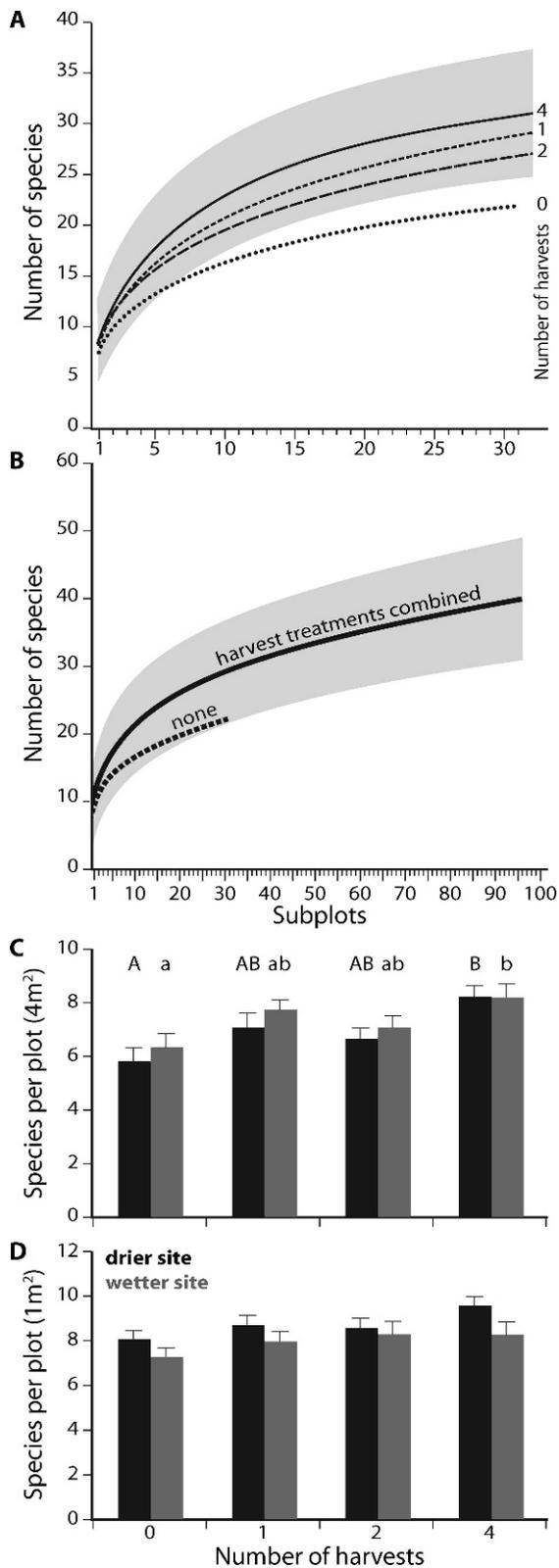


Figure 2. Species richness by treatment in May 2007, one year after the initial harvest. Using rarefaction curves, richness differed between the 4-harvest and control treatments at the wetland scale (including both sites) (A) and between harvest treatments combined and control

($p = 0.06$). Differences were apparently due to reductions of the dominant species *Typha* and *Schoenoplectus* because removal of these species from the distance matrix eliminated differences in composition between harvested and control plots ($R = 0.18$, $p = 0.15$; $R = -0.01$, $p = 0.75$ for the drier and wetter sites, respectively).

In May 2007 (one year post harvest), harvested and control plots differed in composition ($R = 0.34$, $p = 0.03$ and $R = 0.23$, $p = 0.06$ for drier and wetter sites, respectively). Removing the dominant species *Typha* and *Schoenoplectus* did not significantly change these results ($R = 0.36$, $p = 0.02$; $R = 0.36$, $p = 0.04$). However, repeating the analysis after replacing the Bray-Curtis distance matrix with a distance matrix using only species presence/absence eliminated the differences between harvested and control plots ($R = -0.13$, $p = 0.82$), suggesting that ANOSIM differences were due mostly to variation in the relative abundances of species.

Relationships Among Community Composition and Other Factors

A 2-dimensional NMS ordination of May 2007 species cover-class data of both sites combined gave the best combination of stress reduction (stress = 0.13) and interpretability, and it explained 92% of the variation in the distance matrix (Figure 3). Water depth, litter, τ at 1 m and at ground level, and species richness all had $R^2 > 0.35$ with ordination axes, which we defined as a threshold of meaningful correlation with this data (see Figure 3 for relative magnitude of vectors). Plots from both sites segregated clearly along axis 1 (Figure 3), although harvested plots from both sites did not segregate from control plots. Axis 1, best correlating with water depth, explained 85% of the variation of the distance matrix.

Because of the separation of plots from the two sites in ordination space, we also ordinated each site independently. Plots did not segregate by individual harvesting treatment at either site, but control plots did segregate from harvested plots combined (Fig-

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treatments (B). Gray shading = 95% confidence intervals. Richness also differed at the plot (4-m²) scale (C), while richness was similar at the 1-m² subplot scale (D). For C and D, $n = 4$ for each treatment/site combination. Error bars represent ± 1 SE. Treatments with different letters are significantly different within the drier site (upper case) or the wetter site (lower case) according to Tukey's HSD.

ure 3). Three-dimensional ordinations for the drier and wetter sites had stresses of 8.4 and 7.2, respectively, and explained 89% and 91% of the variation in the distance matrix. In the drier site, several variables had $R^2 > 0.35$ with ordination axes: harvesting (as a binary variable), LAI at 1 m and at ground level, τ at 1 m, *Typha* flowering ramet density, a north-south gradient, and species richness at the plot level. LAI and τ at 1 m and harvesting correlated mostly with axis 1; whereas species richness at plot scale and *Typha* flowering ramet density correlated mostly with axis 2; and a north-south gradient and LAI at ground level correlated mostly with axis 3 (Figure 3). Axes 1 and 2 explained 37% and 39% of the variation in the distance matrix, while axis 3 explained 13%. In the wetter site, different variables correlated with ordination axes ($R^2 > 0.35$). Water depth and litter cover had strong correlations with axis 1, while harvesting and LAI and τ at ground level correlated with axis 2 (Figure 3). *Typha* height and density and a north-south gradient closely matched water depth, so were removed for simplicity. Axis 2 explained 55% of the variation in the distance matrix, while axes 1 and 3 explained 11% and 25%, respectively.

Treatment Effects on *Typha* and *Schoenoplectus*

Before the initial harvest, *Typha* height and density strongly differed by site ($F_{1,23} = 24.4$, $p < 0.0001$) but not by treatment ($F_{3,26} = 0.2$ and 0.5 , $p = 0.90$ and $p = 0.70$ for height and density). Five months after the initial harvest, *Typha* in control plots grew to 250 and 350 cm tall in the drier and wetter sites, respectively (Figure 4), while all three harvesting treatments significantly reduced *Typha* height > 100 cm relative to the control at both sites (Table 3). However, harvesting treatments did not differ from each other (Tukey $p > 0.10$). In the wetter site, *Typha* height was reduced proportionally more by harvesting (weak treatment \times site interaction, Table 3). In addition to treatment and site effects, *Typha* height correlated positively with pre-treatment height and relative water depth and negatively with *Typha* density of flowering ramets, all of which were significant co-variates (Table 3). Harvesting also reduced *Typha* density at the wetland scale (Figure 4; ANOVA treatment effect, Table 3), however, harvested plots differed from the control in the wetter site (Tukey p -values < 0.05), but not in the drier site (Tukey p -values > 0.90). Harvesting reduced *Schoenoplectus* height ($F_{3,22} = 33.8$, $p < 0.0001$) and had a larger effect in the wetter site than in the drier site (site \times treatment interaction, $F_{3,22} = 11.3$, $p = 0.0001$).

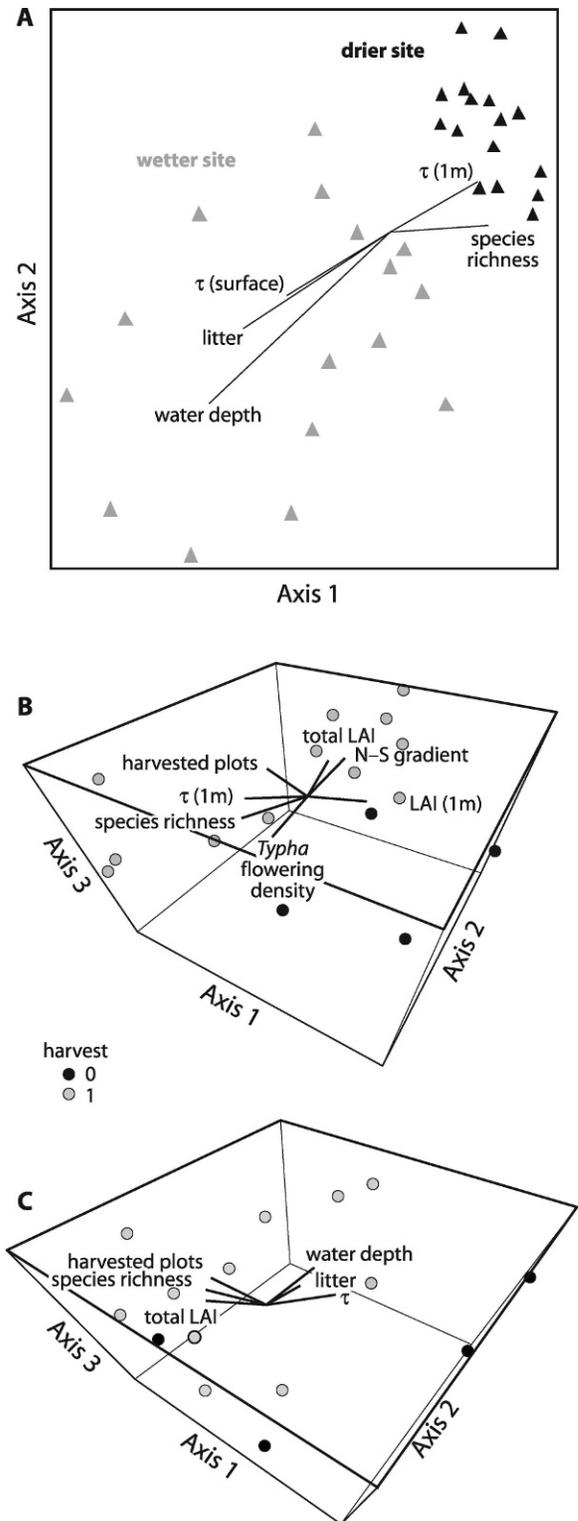


Figure 3. NMS ordinations of plots in species space for A) both sites combined, B) the drier site, and C) the wetter site, showing vectors with $R^2 > 0.35$ with ordination axes. Control plots are in black and harvested plots are in grey in B) and C).

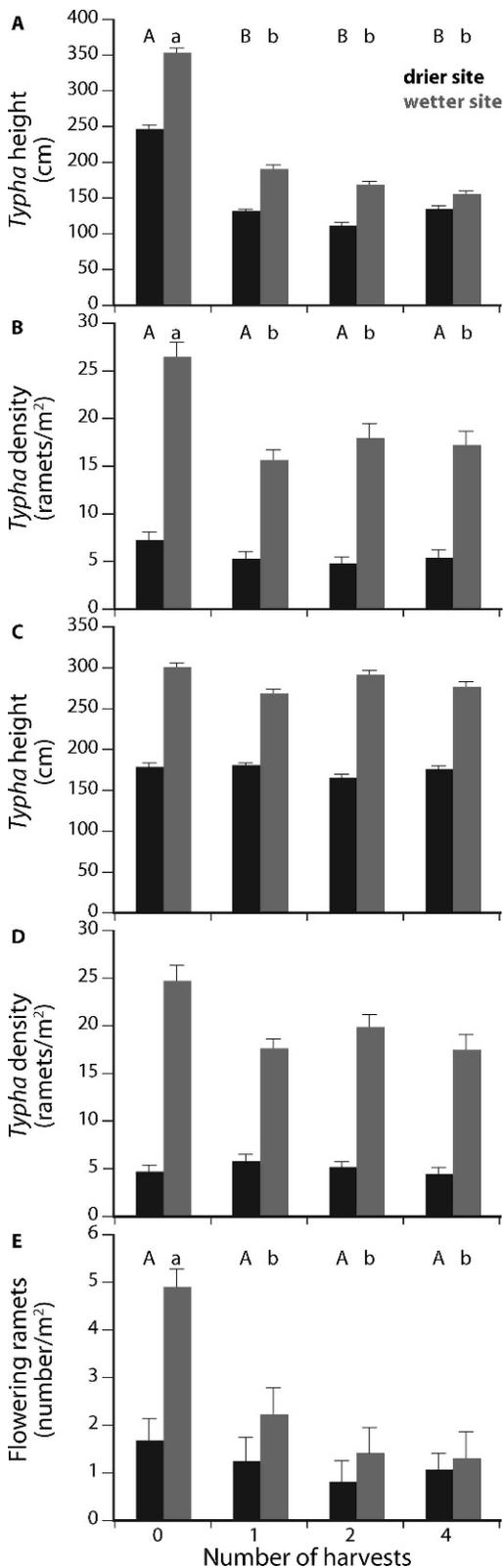


Figure 4. *Typha domingensis* height and density by treatment and site: *Typha* height (A) and density (B) in October 2006, five months after the initial harvest, measured before the fourth harvest; *Typha* height (C) and density (D) and flowering ramet density (E) in May

During the second, third, and fourth harvests of *Typha* re-growth, we harvested an average of 43 ± 3 , 73 ± 3 , and 59 ± 2 g/m² of biomass from the wetter site, and 2 ± 1 , 13 ± 2 , and 31 ± 2 g/m² from the drier site, respectively. By five months after the initial harvest, all harvesting treatments in both sites significantly reduced rhizome starch mass (Figure 5) to less than one-fourth that of the controls ($F_{3,7} = 9.6$, $p = 0.007$), with a weak treatment \times site interaction ($F_{3,7} = 3.7$, $p = 0.07$). The wetter site had significantly greater starch mass than the drier site ($F_{1,7} = 12.2$, $p = 0.01$), and water depth was a significant covariate ($F_{1,7} = 9.0$, $p = 0.02$).

By May 2007 (one year post harvest), *Typha* height was similar between harvested and control plots (Figure 4), and treatments did not differ significantly (Table 3), and harvested plots combined did not differ from control plots ($T_{23} = 1.38$, $p = 0.09$). *Typha* density was similar between harvested and control plots in the drier site, but density appeared lower in the wetter site (Figure 4), although global ANOVA treatment effects were not significant (Table 3). Harvested plots combined had similar density to control plots ($T_{23} = 1.45$, $p = 0.08$). *Typha* remained 1 m taller and four times as dense in the wetter site than in the drier site (Figure 4). In the wetter site, all harvesting treatments significantly reduced flowering ramet density by more than 50% relative to the control (Figure 4, Table 3), whereas in the drier site *Typha* flowering was unaffected by harvesting. Pre-treatment flowering ramet density was significantly correlated with post-treatment flowering ramet density (Table 3). *Schoenoplectus* heights were similar between treatments ($F_{3,22} = 0.1$, $p = 0.96$).

Effects of Harvesting on Canopy Structure in May 2007

One year after the initial harvest treatment, LAI and τ at ground level and 1 m did not differ by treatment ($F_{3,26} < 2.3$, $p > 0.10$). However, when all harvest treatments were combined, we saw a decrease in LAI above 1 m compared to the control in the wetter site (1.7 vs. 2.3, $T_{28} = 1.83$, $p = 0.04$) but not in the drier site (1.22 vs 1.23). LAI at ground level was similar between harvested and control plots (5.5 vs. 4.9 for the drier site, 6.5 vs 5.9 for the

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2007, one year after the initial harvest. Error bars represent ± 1 SE. Treatments with different letters are significantly different within the drier site (upper case) or the wetter site (lower case) according to Tukey's HSD; $n = 4$ for each treatment/site combination.

Table 3. Linear models for *Typha* height and density at the plot scale in October 2006 and May 2007, and flowering ramet density in May 2007.

A) Linear model for <i>Typha</i> height in October 2006				
	d.f.	M.S.	F	p-value
Treatment	3	46731	111.73	< 0.0001
Site	1	30474	72.86	< 0.0001
Relative water depth	1	4123	9.86	0.005
<i>Typha</i> ramets in flower (%)	1	3868	9.25	0.006
Pre-treatment height	1	3271	7.82	0.011
Treatment × site interaction	3	1818	4.35	0.016
Residuals	21	418		
B) Linear model for <i>Typha</i> density in October 2006				
	d.f.	M.S.	F	p-value
Treatment	3	69	4.96	0.009
Site	1	1519	108.59	< 0.0001
Pre-treatment density	1	233	16.66	0.001
Relative water depth	1	9.65	0.69	0.42
<i>Typha</i> ramets in flower (%)	1	46	3.26	0.09
Treatment × site interaction	3	29	2.08	0.13
Residuals	21	14		
C) Linear model for <i>Typha</i> height in May 2007				
	d.f.	M.S.	F	p-value
Treatment	3	430	0.92	0.45
Site	1	98624	211.59	< 0.0001
Relative water depth	1	8735	18.74	0.0003
Pre-treatment height	1	7281	15.62	0.0007
<i>Typha</i> ramets in flower (%)	1	11	0.02	0.88
Treatment × site interaction	3	213	0.46	0.72
Residuals	21	466		
D) Linear model for <i>Typha</i> density in May 2007				
	d.f.	M.S.	F	p-value
Treatment	3	0.07	0.87	0.47
Site	1	14.77	179.53	< 0.0001
Relative water depth	1	0.55	6.74	0.02
Pre-treatment density	1	0.79	9.57	0.006
<i>Typha</i> ramets in flower (%)	1	0.02	0.18	0.67
Treatment × site interaction	3	0.07	0.86	0.48
Residuals	21	0.08		
E) Linear model for <i>Typha</i> flowering ramets in May 2007				
	d.f.	M.S.	F	p-value
Treatment	3	8.30	14.04	< 0.0001
Site	1	13.13	22.21	0.0001
Pre-treatment flowering density	1	6.08	10.29	0.004
Relative water depth	1	0.21	0.36	0.56
Treatment × site interaction	3	3.33	5.64	0.005
Residuals	22	0.59		

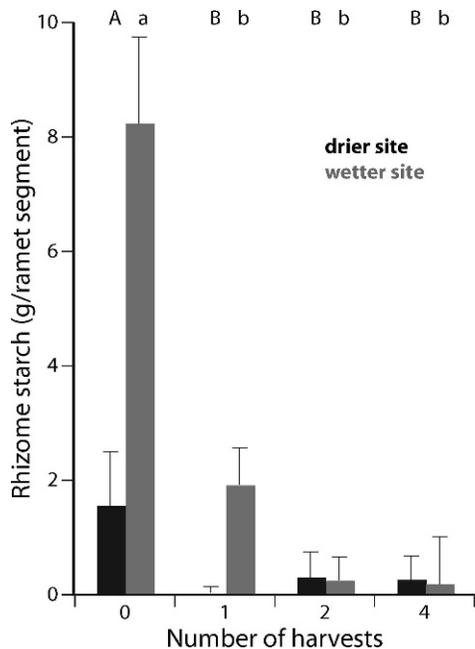


Figure 5. *Typha* rhizome starch mass by treatment five months after initial harvest (sampled before the fourth harvest); $n = 2$ for each treatment/site combination. Rhizomes from harvested plots had significantly less starch than those from the control. Error bars represent ± 1 SE. We used total starch mass per rhizome sample to account for both rhizome mass and starch concentration.

wetter site, $T_{28} = 1.45$, $p = 0.08$). Harvesting did not affect τ at ground level relative to the control (2% vs 2% for the drier site, 3% vs. 4% for the wetter site). Harvesting increased light penetration at 1 m in the wetter site (46% vs 35%, $T_{28} = 1.83$, $p = 0.04$), but not in the drier site (56% vs. 56%).

DISCUSSION

In a win-win conservation project, harvesters would have an economic incentive to remove dominant or invasive plants and harvested sites would respond by supporting more species. Our data suggest that such a situation is possible in central Mexico, where people can find uses or markets for *Typha* leaves. Harvesting increased species richness and the Shannon index at multiple spatial scales, and several sub-dominant species increased in importance. Some species were significantly more likely to be found only in harvested plots than only in control plots, and new species (not initially found at the site) tended to recruit into harvested plots.

One Harvest was Enough to Increase Diversity

Theory predicts that increasing the level of selective herbivory (analogous to our repetitive

Typha harvest treatments) should lower the equilibrium population size of a dominant plant and alter interactions with subordinate plants (Louda et al. 1990). Our one-year results, however, suggest that the initial harvest acted as a meaningful threshold for vegetation change (based on species presence and abundance), beyond which the plant community and *Typha* responded little to additional selective *Typha* harvesting. Plots where we harvested *Typha* re-growth one or three more times after the initial harvest did not differ significantly in terms of richness or composition from plots completely harvested once.

Harvesting Increased Diversity Despite the Recovery of Dominant Plants

Although other studies suggest that high diversity follows from long-term biomass reductions in intensively harvested wetlands (Wheeler and Giller 1982, Verhoeven et al. 1988, Bobbink and Willems 1991), diversity can increase quickly via seedling recruitment in canopy openings (Jutila and Grace 2002) or via vegetative re-growth, even when dominant plants quickly regain their height and density (Denslow 1985, Diemer et al. 2001). Subordinate species can persist among dominant plants if the disturbance return interval is short (Grubb 1977). At Mintzita, increased diversity could have occurred both through recruitment mediated by harvesting and persistent effects on dominant vegetation (e.g., reduced LAI or *Typha* density in the wetter site, Figure 4). In the short term (three months post harvest), we saw no significant responses to harvesting, but one year post-harvest, statistically significant differences developed in composition and species fidelity between harvested and control treatments. In the literature, lag times in plant community response to reduction of dominants range from months (Armesto and Pickett 1985) to years (Güsewell et al. 1988), and probably reflect seasonal constraints on recruitment and the timing of reduction of dominants (Grubb 1977, Armesto and Pickett 1985, Jutila and Grace 2002). In our case, elevated summer water levels or litter accumulation could have limited recruitment until water levels seasonally declined and the February burn removed fallen litter.

Although the lack of a persistent seed bank is often a major constraint on species recruitment after harvesting (Güsewell et al. 1988, Bekker et al. 1997, Smith et al. 2002), the rapid increase in species richness after harvesting at Mintzita suggests that the seed bank was an important propagule source. In fact, several forb species (and *Typha*) emerged in

a pilot seed-bank study of soil from Mintzita (M. Gómez-Romero, UNAM-CIEco, unpublished data). The recent cessation of harvesting at Mintzita, however, might have already eliminated some historically present species (Bekker *et al.* 1997, Linusson *et al.* 1998). We found numerous uncommon and short-statured genera, such as *Eriocaulon* and *Spiranthes*, at a wetland in nearby Zacapu, Michoacán that was otherwise similar to Mintzita in both flora and hydrology (S. Hall, unpublished data); such taxa might have occurred historically at Mintzita.

Community composition and species richness appear influenced by habitat heterogeneity (water levels and litter accumulation) in addition to harvesting. In the drier site, subplot-level species richness correlated well in ordination space with light penetration at 1 m, which only partially correlated with harvesting; in the wetter site, subplot-level species richness correlated more strongly with total LAI than with harvesting. Other manipulations associated with harvesting that we did not measure (e.g., trampling or inconsistencies in harvesting) could also contribute to community variability.

Grasses and “Creeping Emergents” Responded to Harvesting

Grasses increased in importance in harvested plots, both from vegetative re-growth and seedling recruitment (Table 1). The grasses *Andropogon glomeratus*, *Leersia hexandra*, and *Agrostis hyemalis* predominated at Mintzita, and we would expect their perennial life-history and basal meristems to tolerate harvesting (Jameson 1963). *Andropogon glomeratus* is a grazing-tolerant (Capece and Mozaffari 1997), facultative wetland grass that recruited only in harvested plots. A congener (*A. greenwayi* Napper) is known to tolerate and even require grazing to avoid exclusion (McNaughton 1979). Shorter forbs (< 0.5 m tall) also increased in importance in harvested plots as found in other harvesting experiments, presumably because of increased light availability (Armesto and Pickett 1985, Fossati and Pautou 1989, Bobbink and Willems 1991). Several species that significantly increased in importance following harvest belong to Rejmánková's (1992) “creeping emergent” macrophyte guild, characterized by vegetative spread and high relative growth rate after harvesting. *Berula erecta*, *Bidens laevis*, *Hydrocotyle verticillata*, and *Mimulus glabratus* have diverse leaf architectures that differ substantially from the dominant monocots, and could create a more complex canopy

that could explain a tendency towards increased LAI in harvested plots. We observed cut fragments of *B. laevis* rooting and growing vigorously after the initial harvest. *Hydrocotyle verticillata* could potentially avoid damage from harvesting altogether because of its short height (usually < 20 cm); a congener increased in other harvesting experiments (Güsewell *et al.* 1988, Fossati and Pautou 1989). Overall, more species appeared to benefit from harvested conditions than non-harvested. *Galium trifidum* was the only species that showed greater importance in control plots. While increases in local species richness are sometimes associated with the loss of uncommon species and a concomitant decrease in the regional species pool (Keddy 2000), we saw no evidence of this phenomenon at Mintzita.

Almost all new species that we found one year after harvesting were perennials, with three species of unknown life history (Table 1). Some exotic ruderal species (e.g., *Lactuca seriola*, *Polypogon monspeliensis*) were present at low frequency and cover, but their paucity surprised us, especially given the assumption that such species should thrive in disturbed (i.e., harvested) plots (Grime 1979). In harvested wetlands, perennial species often predominate (Wheeler and Giller 1982, Smith and Jones 1991, Fojt and Harding 1995, Ryser *et al.* 1995, but see Hald and Vinther 2000), potentially because frequent harvesting could prevent seed formation in annuals (Smith and Jones 1991). Most of the perennials at Mintzita are capable of vegetative spread (rhizomatous, stoloniferous, or rooting from leaf nodes, Table 1), and they can persist without sexual reproduction. In addition to increasing diversity, it appears that harvesting also benefited species that could potentially withstand further harvesting.

Typha was Resilient to Repeated Harvest

We were surprised by similarities in *Typha* height and density between the harvesting treatments after five months, and also by similarities between harvested and control plots after one year. *Typha* height was not significantly reduced the following year, even though all three harvesting treatments substantially reduced rhizome starch mass. *Typha*'s ability to re-grow could suggest either high photosynthetic rates of new leaf tissue (Jameson 1963) or a clonal subsidy—from older ramets with accumulated reserves inside the plot or from uncut neighbors outside the plot (Pennings and Callaway 2000). A clonal subsidy seems more plausible, since harvested ramets had lower starch reserves in October, and would likely show decreased growth the following

year without a clonal subsidy (Chapin III et al. 1990).

Regardless of the mechanism, *Typha* appeared resilient to our most intensive treatment of four harvests per year. This suggests that the maximum frequency reported by *Typha* harvesters around Lake Pátzcuaro, Michoacán (four times per year; S. Hall, unpublished data), is sustainable, at least in the short term. Local harvesters commonly cut *Typha* above the water surface, as we did. Even though we began our harvesting treatments just before the local rainy season, cut ramets were never flooded by rising water levels, and probably did not experience anaerobic conditions, which are known to damage other *Typha* species (Sale and Wetzel 1983). Repetitive harvesting over successive years, however, might show different results. If a clonal subsidy increases *Typha* re-growth after harvest, it would be important to maintain un-harvested patches. Since harvesting once per year decreased *Typha*'s potential for seed production in the wetter site, and since subtle increases occurred in ramet density in harvested plots from 5–12 months after harvesting (Figure 4) at the same time that flowering ramets decreased (Figure 4), we suggest that resource allocation shifted from sexual to vegetative reproduction (McNaughton 1979). While a reduction in propagule pressure from *Typha* could be desirable from a biodiversity management perspective, the fact that a single flowering ramet can produce 6×10^5 seeds (Howard-Williams 1975) makes even a 50% reduction in flowering ramets unlikely to prevent further invasion from seed.

Conservation Implications

Harvesting has important implications for diversity maintenance at Mintzita, but ordinations implicated additional factors that affect community composition and species richness. Water depth (or a correlate) most influenced community composition at the wetland scale (Figure 3), while harvested plots only segregated from control plots when we ordinated sites individually. We interpret water depth as a more important influence on community composition than harvesting. Harvesting sporadically at multiple sites, rather than intensively harvesting a single site, could increase the likelihood of species responding positively because almost half of the species had a significant site correlation, including some species that appeared to benefit from harvesting (Table 1). Harvesting plot-size patches could allow more species to recruit, especially if the seed bank is spatially heterogeneous and seeds are scarce, because differences in species richness

accrued more at the plot and site scale than at the subplot scale (Table 2). Interspersing harvested and un-harvested vegetation could promote re-growth of *Typha* via a clonal subsidy.

The few wetlands that have escaped cultivation in the altiplano are strong candidates for conservation, given their inherent scarcity in this dry landscape (West 1948). Given the management history of these systems and the resilience of the plant community, we suggest that some harvesting be permitted in conservation areas, rather than prohibited as strict preservationists advocate. Benefits to local people are obvious, since an armful-sized bundle of *Typha* leaves sold for \$1–3 US (in 2007) near Lake Pátzcuaro, Michoacán, where weavers have a high demand for raw materials (S. Hall, unpublished data). Because our experiment tested a subset of harvest regimes that fell within local norms, we suggest that harvesting can contribute to biodiversity conservation.

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