



Removing Duff Layers in Fire-suppressed Wetlands can Aid Habitat Restoration Efforts

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Received: 19 June 2023 / Accepted: 13 September 2023
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Abstract

Amphibians breeding in ephemeral wetlands within pine-dominated (*Pinus* spp.) natural communities are less likely to persist in wetlands that have developed high canopy cover and low herbaceous groundcover in the absence of regular plant growing-season wildfires. The reintroduction of historic fire regimes, in conjunction with mechanical or herbicide removal of woody shrubs, can reduce the woody midstory in wetlands. However, certain conditions can hinder the reemergence of herbaceous groundcover in degraded wetlands even after the removal of the woody midstory. After four years of no discernible recovery of herbaceous vegetation at two Reticulated Flatwoods Salamander (*Ambystoma bishopi*) breeding wetlands, we conducted a duff-removal experiment to test whether duff accumulation was preventing herbaceous plant germination and growth. Using a paired design, we found that duff removal increased the number of sprouting stems by 30-fold compared to control plots (paired t-test: $t_{19}=5.30$; $p<0.001$) and shifted vegetation communities towards more desirable herbaceous groundcover (PERMANOVA: $F_{1,34} = 19.14$; $p<0.001$). Fire is recognized as an important source of disturbance in longleaf (*Pinus palustris*) and slash (*P. elliottii*) pine forests of the southeastern United States, but the return of fire to degraded habitats may not be sufficient to fully restore historic conditions that are conducive to flatwoods salamander reproduction. Our results demonstrate that duff removal may be a critical component of wetland restoration to improve or accelerate the response of understory vegetation following canopy removal.

Keywords *Ambystoma bishopi* · Ephemeral wetlands · Fire ecology · Herbaceous vegetation · Longleaf pine · Reticulated flatwoods salamander

Introduction

The coastal plain of the southeastern United States was historically dominated by longleaf (*Pinus palustris*) and slash (*P. elliottii*) forests and maintained by frequent fire (Stout and Marion 1993; Frost 1995; Provencher et al.

2001). Ephemeral wetlands embedded within the longleaf and slash pine ecosystem are thought to have burned every 3–10 years (Frost 1995; Kirkman 1995). A study examining fire scars in longleaf pine stumps in the Florida Panhandle found that from 1679 to 1868, the average fire return interval was 3.2 years, with 72% of all fires having occurred within one to three-year intervals and 92% within five-year intervals (Huffman 2006). Regular fire acts to exclude or reduce woody growth from wetland basins, resulting in wetlands typically characterized by well-developed herbaceous groundcover and relatively open canopy (Kirkman et al. 1998; Hinman and Brewer 2007; FNAI 2010; Jones et al. 2010). By the early 1930s, however, fire suppression by land managers had become widespread across the southeastern United States (Provencher et al. 2001). We use the language “ecological driver” rather than “disturbance”, as suggested by Askins et al. (2007), to describe continual and pervasive ecological processes as opposed to occasional

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events. In longleaf and slash pine savannas, fire is a driver rather than a disturbance (although infrequent intense fires that occur during droughts might constitute disturbance; Cypert 1961). Following the removal of fire-related drivers in wetland basins, the vegetation shifts to communities that consist of dense canopies, a shrubby midstory, and a notable lack of herbaceous groundcover, becoming fire-resistant rather than fire-maintained (Martin and Kirkman 2009; Palmquist et al. 2014).

Although prescribed fire has been used effectively in recent decades to restore longleaf and slash pine forests towards historical conditions (Provencher et al. 2001), many wetlands embedded within these ecosystems have been inadequately restored because prescribed fire is frequently applied outside the plant-growing season (e.g., late fall – early spring), when ephemeral wetlands are most likely to be inundated with standing water (Bishop and Haas 2005; Knapp et al. 2009; Chandler et al. 2016). Prescribed burning outside the plant-growing season results in the accumulation of recalcitrant litter and loss of fine fuels as herbaceous vegetation is eliminated, which can prevent fire from entering wetland basins. Therefore, even at regularly burned sites, vegetation communities may not return towards historical conditions (Martin and Kirkman 2009; Gorman et al. 2013). Lack of seed source is one potential reason why herbaceous vegetation does not return following burns, particularly at isolated sites (Kettenring and Galatowitsch 2011). Alternatively, the build-up of a significant duff layer over the long history of fire suppression/exclusion in these wetlands may prevent the reemergence of herbaceous plant communities, even after the woody midstory is removed (Cypert 1961; Gorman et al. 2013). Thus, there is a need to understand the drivers of vegetation dynamics in instances where restoration efforts are only partially successful. With such information, it will be possible to evaluate what combination of management techniques can best replicate the natural disturbance regime and more fully restore vegetation communities in ephemeral wetlands.

We conducted an experimental study to evaluate the impact of duff removal on wetland vegetation characteristics in pine flatwoods wetlands. This work is part of ongoing habitat restoration efforts for the federally endangered Reticulated Flatwoods Salamander (hereafter flatwoods salamander), *Ambystoma bishopi*, on Eglin Air Force Base, Florida. Flatwoods salamanders occur in mesic longleaf and slash pine-dominated habitats and migrate to ephemeral wetlands in the fall to lay eggs in dry wetland basins (Anderson and Williamson 1976). Aquatic larvae hatch from the eggs once fall and/or winter rains inundate the wetland. The larvae shelter among herbaceous plants and feed predominantly on aquatic invertebrates (Whiles et al. 2004; Brooks et al. 2019), taking approximately 3.0–4.5 months

(depending on water temperature and food availability) to grow and develop to metamorphosis (Palis 1995; Brooks et al. 2020). Flatwoods salamanders occupy only a fraction of their former range, with loss of suitable breeding wetlands cited as a primary factor in their decline (USFWS 2009). To date, habitat restoration has primarily involved the reintroduction of natural fire regimes through prescribed fire and the mechanical and herbicide removal of woody vegetation from wetland basins (to act as a surrogate for fire). However, there is evidence that current restoration practices may not be sufficient for the re-establishment of complex and stable herbaceous plant communities (Gorman et al. 2013; Gorman and Haas 2014). Our objectives were to evaluate whether duff layers are responsible for the suppression of herbaceous groundcover regrowth, and to measure the response of this vegetation following targeted duff removal.

Materials and Methods

Study Area

Our study area was located at Eglin Air Force Base (Eglin) in Okaloosa and Santa Rosa counties in northwestern Florida. Eglin is a large military installation that spans > 187,000 ha. The topography of the study area is level to rolling, with the highest elevation at ~75 m and slopes that generally range from 0 to 30% (Eglin Air Force Base 2002). Most of the upland habitat on Eglin is a longleaf pine and turkey oak (*Quercus laevis*) sandhill community. However, our study focused on 25 ephemeral wetlands (ranging in size from 0.3 to 5.9 ha) located on the western portion of Eglin, usually surrounded by wet or mesic pine flatwoods. All wetlands were either occupied by flatwoods salamanders or considered potential breeding wetlands for flatwoods salamanders based on habitat surveys conducted by Florida Natural Areas Inventory and the present authors (e.g., Gorman et al. 2009).

Experimental Design

The wetlands included in this study were part of previous restoration efforts for flatwoods salamanders (Gorman et al. 2013; Gorman and Haas 2014). In 2010, 25 wetlands were selected for restoration based on the condition of their midstory and locations in areas where prescribed fire could be applied. Sites received either mechanical removal of woody vegetation and a targeted cut-stump application of herbicide, a wetland basin burn, or both. Vegetation was sampled before and after treatments to evaluate if habitat management practices improved the habitat conditions for flatwoods salamanders and the broader wetland community

(see Gorman et al. 2013 for details). However, across all treatment groups, limited changes to the herbaceous groundcover community were documented.

To better understand the lack of herbaceous groundcover regrowth following the initial treatments (Gorman et al. 2013; Gorman and Haas 2014), we conducted a follow-up experiment at two of the treated sites. Both sites received similar treatments of mechanical removal of hardwoods with cut-stump herbicide application. Site 1 was included in prescribed fire operations in 2012 and 2013, but neither burn resulted in fire entering the extensive unvegetated basin areas where our raking and control plots were set up. Site 2 remained unburned until August of 2014 when fire carried through the entire wetland basin. In both cases, a significant duff layer persisted (7–12 cm at Site 1, 2–7 cm at Site 2), inhibiting herbaceous growth. In October 2014, we established 40 1 × 1 m plots (20 per wetland) in areas of the wetlands that contained extensive patches of substrate that were either devoid of ground cover or had nothing other than senesced bryophytes (i.e., *Sphagnum* sp.). We established two parallel lines of paired plots that were separated by at least 0.5 m. Plots were considered unsuitable if they included any live or dead stems, or if there was any coarse woody debris that could not be moved without disturbing or exposing soil under the leaf litter (i.e., embedded). Each plot was marked with pin flags in each corner. We randomly denoted which of the pair would be treated (10 raked and 10 unraked at each wetland). Thus, each treated plot had an adjacent, paired untreated plot. No pair of plots was separated by > 1.5 m. Treated plots were raked to a depth of 2–12 cm, depending on depth of duff, until the exposed substrate consisted of a mix of mineral soil and fine particles of organic material that did not include recognizable leaves or twigs. Raked material was always removed in a direction away from untreated plots to avoid confounding results. We defined duff as soil horizons Oi and Oe, or the combination of litter and moderately decomposing parts of plant material that is above the surface of the sapric soil layer, Oa (Federer 1982; Ditzler et al. 2017).

In late May 2015 (approximately seven months post treatment), we returned to the study plots to record plant sprouting and growth while the wetland basins were dry, and all sprouts could be counted and measured. At each plot, we counted the total number of individual plants that had sprouted. We then identified each plant to the lowest taxonomic level possible and then broadly grouped all plants into either “herbaceous” or “woody.” Any stems found in plots that appeared to be a result of vegetative spreading from already existing plants outside the plot were documented but not counted or included in the analysis. To estimate duff depth, we made a sharp vertical cut at the center of the edge of each unraked plot nearest to its paired raked

plot and excavated a divot (~ 10 cm diameter) to allow us to see and measure the depth from the surface to the transition to the Oa horizon, above predominantly mineral soil. Duff depth measurements were recorded to the nearest 0.5 centimeter.

Statistical Analysis

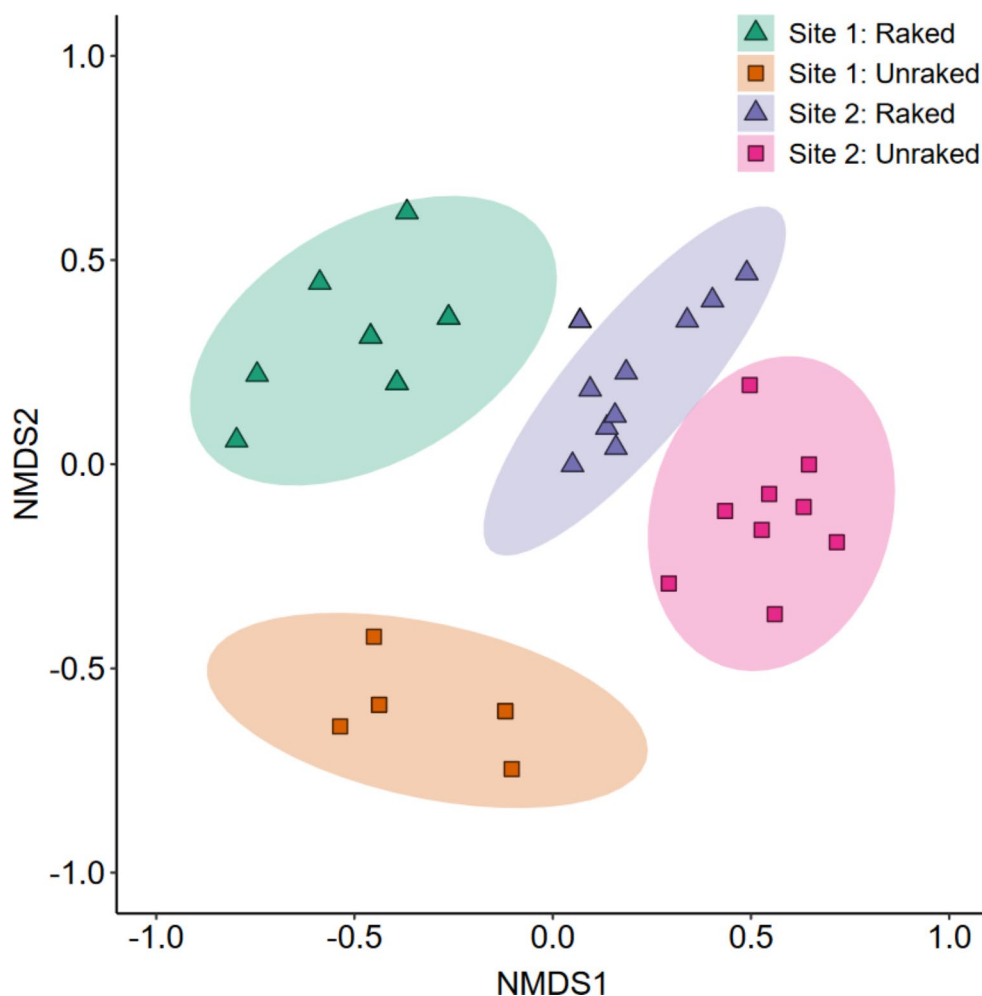
We visualized the vegetation response between raked and unraked plots in each wetland using a non-metric multidimensional scaling (NMDS) plot. NMDS plots were created using Bray-Curtis dissimilarities, and we used a distance-based permutational multivariate analysis of variance (PERMANOVA) to test for differences among treatments and between the two wetlands. For this analysis, plots with no sprouting stems cannot be included. We conducted the PERMANOVA using Bray-Curtis dissimilarity indices to calculate distances with 999 permutations. Additionally, we performed a paired t-test to compare the total count of stems, total count of woody stems, and total count of herbaceous stems between raked and unraked plots (pooling data across sites). All analyses were conducted in R using the *vegan* and *BiodiversityR* packages (Oksanen et al. 2015; R Core Team 2023).

Results

Herbaceous sprouts identified in plots included Golden Crest (*Lophiola aurea*), Grassleaf Goldenaster (*Pityopsis oligantha*), Beaksedge (*Rhynchospora careyana*), Beaksedge (*Rhynchospora* spp.), Yellow-eyed Grass (*Xyris* spp.), Carolina Redroot (*Lachnanthes caroliniana*), Dwarf Umbrella Sedge (*Fuirena pumila*), Dogfennel (*Eupatorium capillifolium*), Witchgrass (*Dichanthelium* spp.), Chalky Bluestem (*Andropogon virginicus* var. *glaucus*), Bluestem (*Andropogon* spp.), and Aster (*Aster* spp.), along with one unidentified herb and one unidentified sedge. Woody sprouts in plots were Wax Myrtle (*Morella cerifera*), Swamp Gum (*Nyssa biflora*), Slash Pine (*Pinus elliotii*), Earleaf Greenbrier (*Smilax auriculata*), Laurel Greenbrier (*Smilax laurifolia*), Pond Cypress (*Taxodium ascendens*), Myrtle Dahoon (*Ilex cassine* var. *myrtifolia*), Large Gallberry (*Ilex coriacea*), Holly (*Ilex* spp.), St. John’s-wort (*Hypericum* spp.), Apalachicola St. John’s-wort (*Hypericum chapmanii*), and Groundsel Tree (*Baccharis halimifolia*).

We found a clear signal for the effect of raking on species composition (PERMANOVA: $F_{1,34} = 19.14$; $p < 0.001$; Fig. 1). Five herbaceous species and three woody species were only documented in raked plots (Table 1). Three herbaceous species and four woody species were only documented in unraked control plots (Table 1). There was also

Fig. 1 Non-metric multidimensional scaling of plant species (woody and herbaceous) in two wetlands that received raking treatments in fall 2014. Each point represents a sampling plot, and points that are closer together have plant community compositions that are more similar than points that are farther apart. The ellipses represent the smallest two-dimensional region that encapsulates 95% of the variation within each site/treatment. Treatment plots with no sprouting stems cannot be shown



evidence for differences in species composition across the two wetlands (PERMANOVA: $F_{19}=10.71$; $p=0.004$). Along with differences in community composition across treatments, we observed a dramatic difference in the number of stems sprouting at raked plots compared to unraked control plots (Figs. 2 and 3). The total number of stems in raked plots was nearly 30 times higher than in unraked control when accounting for site ($t_{19}=5.30$; $p<0.001$). This difference persisted when woody stems ($t_{19}=5.87$; $p<0.001$) and herbaceous stems ($t_{19}=3.56$; $p=0.002$) were analyzed separately.

Discussion

The results of our study indicate that, for ephemeral wetlands in longleaf and slash pine ecosystems, mechanical treatments designed to remove accumulated duff and promote germination in understory seed banks may be an effective tool to restore native herbaceous vegetation communities. Habitat management goals for flatwoods salamanders and several other imperiled species that inhabit these wetlands

were more fully realized with targeted duff removal than by only reducing canopy cover (by either mechanical or prescribed fire). Because herbaceous groundcover is a critical component of larval flatwoods salamander habitat (Gorman et al. 2009, 2014; Jones et al. 2012; Chandler et al. 2017), restoration of habitats that have crossed ecological thresholds into shrub-dominated systems will likely need to go beyond midstory removal (Martin and Kirkman 2009).

Wetlands that undergo regular burn intervals typically support higher species diversity than fire-suppressed wetlands (Russell et al. 1999; Means et al. 2004; Bishop and Haas 2005; Huffman 2006; Jones et al. 2010). Particularly for amphibians that utilize ephemeral wetlands for breeding, fire-maintained conditions are essential for their continued survival (deSzalay and Resh 1997; Skelly et al. 2002; Sacerdote and King 2009; Shulse et al. 2012; Chandler et al. 2015, 2017; Jones et al. 2018). Many amphibians endemic to the longleaf and slash pine ecosystem are now rare, in part due to fire exclusion (Sekerak et al. 1996; Gorman et al. 2009). Prescribed fire is the most common management technique applied in ephemeral wetlands of longleaf and slash pine forests to promote the growth of native herbaceous plant

Table 1 Documented presence of herbaceous and woody plant species in control and treatment plots at two amphibian wetlands in Florida

	Site 1		Site 2	
	Control	Treatment	Control	Treatment
Herbaceous				
<i>Lophiola aurea</i>				✓
<i>Pityopsis oligantha</i>			✓	
<i>Rhynchospora corniculata</i>				✓
<i>Rhynchospora</i> spp.	✓		✓	✓
<i>Xyris</i> spp.	✓			✓
<i>Lachnanthes caroliniana</i>			✓	✓
<i>Fuirena pumila</i>			✓	
<i>Eupatorium capillifolium</i>			✓	✓
<i>Dichantheium</i> spp.			✓	✓
<i>Andropogon virginicus</i>			✓	✓
<i>Andropogon</i> spp.			✓	✓
<i>Aster</i> spp.			✓	
Unknown herb		✓		
Unknown sedge				✓
Woody				
<i>Myrica cerifera</i>			✓	✓
<i>Nyssa sylvatica</i>	✓	✓		✓
<i>Pinus elliotii</i>	✓	✓	✓	✓
<i>Smilax auriculata</i>	✓			
<i>Smilax laurifolia</i>	✓			
<i>Taxodium ascendens</i>		✓		
<i>Ilex myrtifolia</i>	✓	✓	✓	✓
<i>Ilex coriacea</i>				✓
<i>Ilex</i> spp.			✓	
<i>Hypericum chapmanii</i>		✓	✓	✓
<i>Hypericum</i> spp.				✓
<i>Baccharis halimifolia</i>			✓	

communities; however, in some cases, additional methods may be necessary to limit, stop, or reverse habitat degradation and amphibian declines (Watts et al. 2015). Even at regularly burned sites, vegetation communities may not quickly return towards historical conditions, or may need additional management interventions (Fowler 1988; Hiers et al. 2007). Supplementing a diminished seed source may need to be considered at isolated sites or at sites where neighboring wetlands are equally degraded and thus do not contain the desired plant community. Whilst this has not been necessary at the two sites described in this paper, it has proven useful at several other sites in our study area (Jones, *pers. comm.*).

Given that regular burns are a natural component of these ephemeral wetlands, some land managers have suggested that the primary duff layer should be removed by

fire (Cypert 1961). However, removing the duff layer with fire alone may be challenging or even impossible at certain wetlands given their current degraded state; the lack of fine fuel to carry a fire through the wetland basin and the depth of the duff layer can both act to render fire ineffective (Gorman et al. 2013). Following the initial mechanical removal of woody vegetation at the two wetlands in this study, both were exposed to several prescribed fires (including one targeted basin burn in 2014), yet still the duff layer remained largely unaffected. Prescribed fire is usually avoided during conditions that could ignite duff because of the possible negative effects of smoldering fires or muck fires (Varner et al. 2007; Watts and Kobziar 2013; Watts et al. 2015; Kreye et al. 2016). Working with land managers to develop an effective use of fire in wetlands, as well as alternative duff removal efforts, will be important for ongoing restoration efforts (Watts and Kobziar 2013; Watts et al. 2015). Caution must be taken not to inadvertently reduce moist refugia within wetlands that amphibians and invertebrates rely on; scattered woody debris and networks of crayfish burrows likely represent the historically available refugia for this type of wetland (Anderson and Williamson 1976). Understanding the relationships between vegetation cover, soil characteristics, and wildlife in finer detail will be useful to quantify the scale of habitat work necessary to successfully manage focal wetland species, and therefore identify which management strategies are most appropriate.

Although both sites in this study benefited from duff removal, there was a marked difference in the sprouting success in unraked plots. This difference is presumably related to the major difference in fire history within the wetland basins. Site 1 was contained within fire operations in the years preceding this experiment, but fire never penetrated to the areas where raking plots were established. As a result, because there was no prior mechanism for removing the smothering effect of litter, there was very little sprouting in the control plots. Site 2, in contrast, had complete fire coverage across the entirety of all raking and control plots immediately prior to the experiment. Other than the fresh needle and leaf cast from the scorched pine and cypress overstory, there was virtually no litter at this site. The availability of nutrients from the ash may have also increased seedling growth and survival. Moreover, even though there was still a substantial duff layer that remained unconsumed in the basin, it was shallower and thus allowed more seeds to sprout in the unraked control plots compared to Site 1. At the present time, however, we can only speculate on the reasons for site-specific differences. Importantly, the treatment effect was striking at both sites, suggesting that duff removal is beneficial across a range of starting conditions.

Of note, the current plant composition in the wetland basins of both sites used in this study now represents natural

Fig. 2 Comparison of one pair of raked (left) and unraked (right) plots. The photo was taken seven months after duff removal

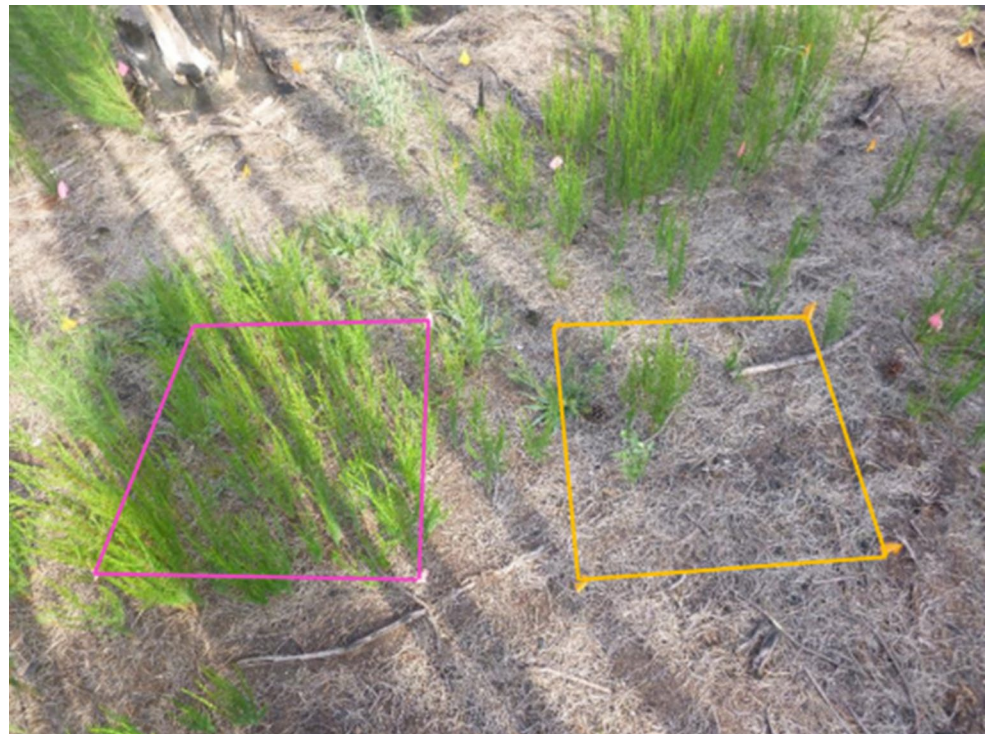
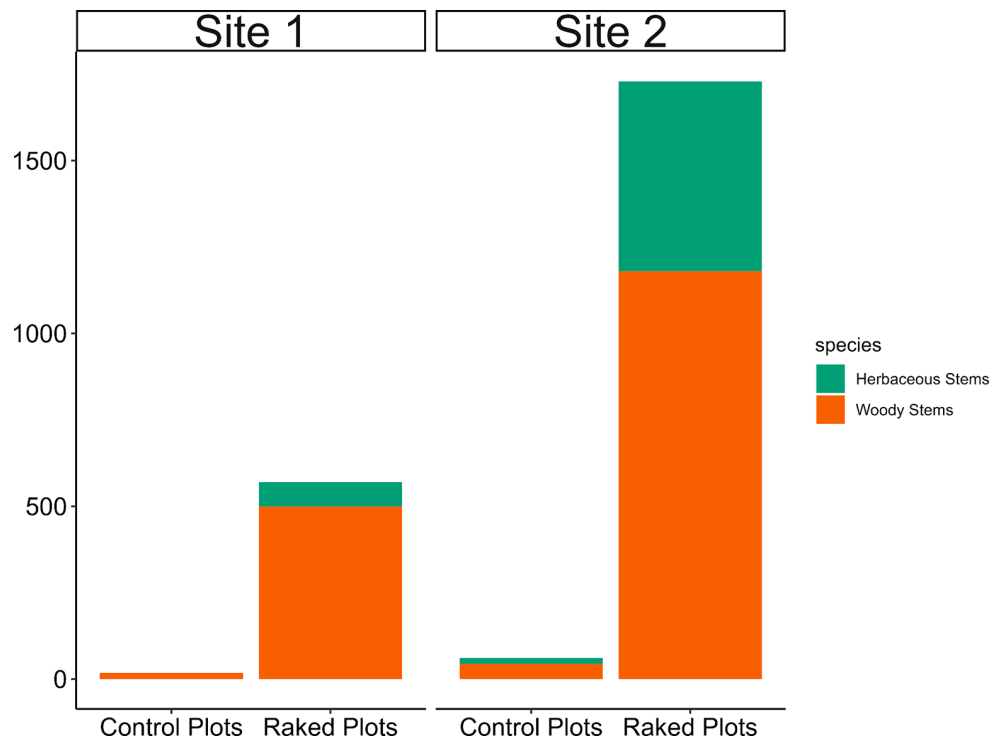


Fig. 3 The number of woody and herbaceous stems in raked and unraked plots at two pine flatwoods wetlands on Eglin Air Force Base. Raking occurred in October 2014, and stem counts were conducted in May 2015. Stem counts are summed across 20 replicates in each site/treatment



plant communities associated with flatwoods salamander breeding habitat. This includes the areas contained in both raked and unraked plots with no further raking beyond what we describe in this paper. This has been achieved by (1) a substantial reduction in canopy cover, (2) oxidation of the duff layer to allow seed germination, (3) targeted use of

prescribed fire every 2–3 years wherever consumption of fine fuels favored survival of perennial herbaceous species over pioneering herbaceous or woody species, and (4) use of brush saws and repeated foliar herbicide treatments to control woody resprouting. This has allowed graminaceous ground cover to serve as a continuous fine fuel layer for

carrying fire capable of thinning young woody plants. Thus, we ultimately advocate for a holistic approach to wetland restoration and management, where the greatest successes will be achieved when several integrative techniques are used together.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s13157-023-01739-7>.

Acknowledgements We thank the Natural Resources Branch of Eglin Air Force Base (Jackson Guard), the Department of Defense Legacy Resource Management Program, the Aquatic Habitat Restoration and Enhancement Program of the Florida Fish and Wildlife Conservation Commission, the U.S. Fish and Wildlife Service, and the Department of Fish and Wildlife Conservation at Virginia Tech for logistical and financial support. We thank S. Goodman for assistance with field work, and B. Hagedorn, J. Johnson, K. Gault, and J. Preston for their long-term support and input on all aspects of this project.

Author Contributions The original study design was developed by Thomas Gorman and Carola Haas. Kelly Jones, John Himes, and Michael Sisson assisted with refinement of hypotheses and management approaches. Data collection and field coordination was conducted by Kelly Jones, Thomas Gorman, and Brandon Rincon. George Brooks, Houston Chandler, and Thomas Gorman performed the analyses. All authors contributed to writing and reviewing drafts of the manuscript. All authors read and approved the final manuscript.

Funding The authors received funding from government awards sponsored by Eglin Air Force Base and the Department of Defense Legacy Resource Management Program, issued by the U.S. Fish and Wildlife Service through Cooperative Agreement #F14AC00068 and the Army Corps of Engineers through Cooperative operative agreement #W9132T-14-2-0008.

Data Availability All data and code needed to perform the analyses are available as electronic supplementary material.

Declarations

Conflict of Interest The authors have no relevant financial or non-financial interests to disclose.

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