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Plant community shifts caused by feral swine rooting devalue Florida rangeland



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ABSTRACT

Invasive species threaten agriculture by changing agroecosystem structure and function, reducing habitat value, decreasing biodiversity and ecosystem services and increasing management costs. Grazing lands in south central Florida are a mosaic of sown pastures, native grasslands, wetlands and woodlands that provide a variety of ecosystem services. Disturbance of these pastures and native grasslands by invasive feral swine (*Sus scrofa*) can have negative consequences for both economic productivity and biodiversity. In this study, we show that the effect of rooting on plant diversity depends on ecosystem type and initial levels of plant species diversity. For example, in native grassland pasture, rooting was initially associated with declines in plant species richness, while in sown pastures, rooting was associated with more sustained increases in plant species richness. In both sown pastures and native grasslands, swine rooting altered plant community composition reducing agricultural productivity. Forage grasses were primarily associated with unrooted areas, whereas low quality forage species or nuisance species were found in rooted areas. We provide an example of monetary losses that cattle ranches can incur when feral swine are abundant on the landscape and control is minimal. Ranch managers and government agencies are encouraged to consider implementing more stringent feral swine management programs to minimize negative effects of feral swine rooting on ecological and economic value of grazing lands.

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1. Introduction

Non-native vertebrates threaten agricultural systems (U.S. Congress, 1993) and the ecosystem services they provide (Kenis et al., 2009; Richardson and Van Wilgen, 2004). In North America, feral swine (*Sus scrofa*) are a non-native species that act as ecosystem engineers (Crooks, 2002; Cuevas et al., 2010; Hone, 2002). Rooting behavior—in which feral swine turn over soil in search of food items—causes soil disturbance and creates opportunistic habitats for disturbance-adapted plants to exploit. The new community composition of these habitat patches may form alternative, yet stable ecological states that are difficult to restore once established (Firn et al., 2013).

Rooting by feral swine has been shown to decrease plant cover (Singer et al., 1984), including forage grasses for cattle and livestock (Tisdell, 1982), and to alter plant communities (Siemann et al., 2009). The resulting opportunistic plant communities include undesirable plants of little value to agriculture, i.e., they are sometimes toxic to livestock, costly to manage or eliminate, and compete with economically important grasses (Baker, 1974). In the southeastern USA, feral swine facilitate the expansion of a native plant species, Carolina redroot (*Lachnanthes caroliniana*), that has been documented as a native invader in commercial cranberry (*Vaccinium* spp.) bogs in Louisiana (Robertson, 1976). In Florida, Carolina redroot has been shown to invade and dominate natural habitats after feral swine rooting, both in experimental plots (Boughton and Boughton, 2014) and in natural systems (C. Gates, pers. comm.).

Plant community responses to rooting by feral swine differ widely among ecosystems, and are in part determined by the life history of resident species as well as other natural and introduced disturbance regimes (Cushman et al., 2004; Kotanen, 1995). Reduced plant species richness has been documented after feral

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swine rooting in native gray beech (*Fagus grandifolia*) forest habitat in the Great Smoky Mountains National Park (Bratton, 1975), but an increase in plant species richness has been observed in California grasslands (Cushman et al., 2004; Kotanen, 1995) and Florida flood plain assemblages (Arrington et al., 1999). Cattle ranches in south central Florida contain a mosaic of high diversity native grassland and low diversity sown pastures and we expected these two communities to respond to disturbance differently.

Our objectives were to document if feral swine rooting caused changes to community composition in native grassland and sown pasture, to determine the resilience of these grassland habitats to rooting disturbance, and to calculate the annual economic cost of lost forage to ranchers. We hypothesized high quality forage would be reduced by rooting in the two dominant pasture types found in Florida, although the mechanisms driving the loss would be different. In native grassland pastures, plant diversity would decrease in areas disturbed by rooting due to invasion of Carolina redroot following disturbance (Boughton and Boughton, 2014). We hypothesized that the composition of communities would also change such that disturbance-adapted plants would be more abundant in rooted areas than in areas that had not been disturbed by feral swine. We predicted that both the decrease in species richness and change in community composition would decrease the abundance of forage grass in native grassland. In sown pastures, where plant diversity is low, we hypothesized that plant diversity would increase after rooting disturbance, as rooting has been shown to interrupt the competitive dominance of non-native grasses (Cushman et al., 2004).

The cost of feral swine damage and control in the United States exceeds \$1.5B annually (USDA, 2013). In Florida, feral swine have been documented to damage imperiled ecosystems as well as agricultural ecosystems costing the state millions of dollars per year (Engeman et al., 2003, 2004, 2007). Florida rangeland provides extensive ecosystem services, has high conservation value and is a direct economic benefit to local and state economies. Based on our estimated loss of forage to rooting, we calculated a baseline estimate of economic losses to cattle ranchers both locally and regionally.

2. Materials and methods

2.1. Study site

The MacArthur Agro-ecology Research Center (MAERC; a division of Archbold Biological Station) spans 4170-ha in Highlands County, Florida, and is one of the top 20 cattle producers in the state. Between 1950 and 1970, ranch owners converted most of the upland dry prairie to sown pasture (~1800 ha), planting Bahia grass (*Paspalum notatum*) to support cattle. Today, the vegetation in the low lying wet prairies of the ranch is generally native and used for winter cattle grazing (~2282 ha). Native grassland pastures primarily consist of medium-quality winter forage grasses including broomsedge (*Andropogon virginicus*), panic grass (*Panicum longifolium*), maidencane (*Panicum hemitomon*), and carpetgrass (*Axonopus fissifolius*). Common forbs include Carolina redroot, coinwort (*Centella asiatica*), thistle (*Cirsium* spp.), and sedges (*Cyperus* spp.). Dog-fennel (*Eupatorium capillifolium*) is a common and problematic woody dicot in these pastures that can cause dehydration in cattle if consumed in large quantities (Ferrell and MacDonald, 2005). In sown pastures, Bahia grass, a common high-quality forage grass in the southeastern United States, dominates; but small amounts of Bermudagrass (*Cynodon dactylon*), another high-quality forage grass, is also present. Forbs include thistle (*Cirsium* spp.) and dog fennel (*E. capillifolium*, Table 1) and other graminoids include sedges (*Cyperus* spp.).

Table 1

List of plant species commonly encountered in this study.

Scientific name	Growth habit	Forage quality
<i>Axonopus fissifolius</i>	Graminoid	Low
<i>Panicum longifolium</i> Torrey	Graminoid	Low
<i>Spartina bakeri</i>	Graminoid	Low after burned
<i>Andropogon virginicus</i> L.	Graminoid	Medium
<i>Panicum hemitomon</i>	Graminoid	High
<i>Paspalum notatum</i>	Graminoid	High
<i>Cynodon dactylon</i>	Graminoid	High
<i>Cirsium</i> spp.	Forb	Unpalatable
<i>Cyperus</i> spp.	Forb	Unpalatable
<i>Lachnanthes caroliniana</i>	Forb	Unpalatable
<i>Sporobolus indicus</i>	Graminoid	Unpalatable
<i>Eupatorium capillifolium</i>	Woody dicot	Unpalatable
<i>Rubus leucodermis</i>	Woody dicot	Unpalatable
<i>Bidens mitis</i>	Forb	Unknown
<i>Centella asiatica</i>	Forb	Unknown
<i>Diodia virginiana</i>	Forb	Unknown
<i>Hydrocotyle umbellata</i>	Forb	Unknown
<i>Justicia angusta</i>	Forb	Unknown
<i>Ludwigia octovalvis</i>	Forb	Unknown
<i>Ludwigia repens</i>	Forb	Unknown
<i>Phyla nodiflora</i>	Forb	Unknown
<i>Rhexia</i> spp.	Forb	Unknown
<i>Bacopa caroliniana</i>	Forb	Unknown
<i>Euthamia minor</i>	Forb	Unknown
<i>Proserpinaca palustris</i>	Forb	Unknown
<i>Eleocharis vivipara</i>	Graminoid	Unknown
<i>Rhynchospora</i> spp.	Graminoid	Unknown
<i>Euthamia graminifolia</i>	Woody dicot	Unknown

Feral swine populations in the Kissimmee River Valley in south central Florida, where MAERC is located, have been documented since the 1840s, and populations were reinforced by escaped free-range domestic swine (Mayer and Brisbin, 2008). Feral swine provide income in this area today; many land managers offer guided hunts or trap feral swine to sell to other land managers for hunting opportunities. Feral swine are abundant on MAERC, with 200–400 individuals sold or hunted annually during 2007–2012 (Boughton and Boughton, 2014), generating approximately \$12,000–\$20,000 per year in revenue. Although feral swine generate income locally and provide food and sport, stakeholders are concerned about the adverse impacts feral swine can have on human, livestock, and wildlife health.

2.2. Experimental design and sampling

We compared plant community composition through time of rooted and unrooted pastures using a permanent paired subplot design. We began estimates of community composition one month after feral swine rooting in both native and sown pastures. Monthly sampling of plant community composition occurred in sown pastures for 13 consecutive months, April 2013–April 2014. In native grassland pastures sampling occurred from March to June 2013, and from October 2013 through April 2014 for a total of 11 sampling months. We were unable to complete sampling in July, August, and September of 2013 due to extensive flooding.

In order to define rooted and unrooted patches, we mapped rooted areas. In two native grassland pastures we established six 100m transects per 30-ha pasture; in sown pastures, we established four 100m transects in each of two 20 ha pastures. We mapped all freshly rooted patches that fell along transect lines that were 4 m² or greater in area using a Trimble GeoXT. Among the mapped rooted patches we randomly chose 24 rooted patches and established four subplots per patch for permanent vegetation sampling in native grassland pastures and eight rooted patches with four subplots per rooted patch in sown pastures. Each subplot within rooted areas was paired with a neighboring unrooted

subplot that had the same soil type (NRCS, 2006) and similar elevation (National Elevation Dataset, 2011). Plant species composition and canopy cover of each species was recorded monthly in the paired subplots using six cover class system (1:0–5%, 2:5–25%, 3:25–50%, 4:50–75%, 5:75–95%, 6:95–100%; Daubenmire, 1959). The midpoints of each cover class were used as % cover values for statistical analysis. Cover was also recorded for litter, bare ground, and water. Forty subplots in the native grassland pastures were burned in an escaped prescribed burn during March 2013 and were excluded from the study. In total, we sampled 152 subplots in 19 patches in native grassland pastures ($n = 76$ rooted and $n = 76$ unrooted) and 64 subplots in 8 patches in sown pastures ($n = 32$ rooted and $n = 32$ unrooted).

2.3. Statistical analyses

We averaged species richness among subplots within rooted patches and within their paired counterparts outside rooted areas to understand the effect of rooting on species richness. Species richness was defined as the number of unique species (program PC-ORD version 6.0). Permanent subplots are excellent for tracking temporal changes (Lesica and Steele, 1997), but datasets are not statistically independent from month to month. We therefore ran two-way repeated measures analyses of variance (ANOVA) in SigmaPlot (version 11.0) and compared pairwise measures of diversity among sampling months and rooted patches using Holm–Sidak multiple comparison procedures.

We used nonmetric multidimensional scaling (NMS) in program PC-ORD (version 6.0) to investigate how rooting influenced plant species composition. As this type of analysis has few assumptions, it is appropriate for repeated measures of ecological data. We ran two separate ordinations, one for each pasture type. The native grassland ordination included percent cover measurements of 23 plant species, bare ground, litter, and water in a total of 1672 subplots (152 plots over 11 sampling events). The sown pasture ordination included percent cover measurements of 18 plant species, bare ground, litter, and water

from 832 subplots (64 plots over 13 sampling events). We ran the analyses on autopilot mode, which included a random starting point, 250 runs with real data, 250 runs with the data randomized (Monte Carlo test), and 500 iterations. We used Sørensen's distance, defined as shared abundance divided by total abundance (McCune et al., 2002), to calculate the dissimilarity matrix. We chose the best solution to each ordination by comparing the final stress value, a measure of goodness of fit, to dimensionality. Final stress values generated from data were lower than the final stress in 95% of the randomized runs.

We conducted permutational multivariate analyses of variance (PerMANOVA) in PCORD (version 6.0) to determine significant differences in plant species composition in rooted vs unrooted subplots (Anderson and Braak, 2003). This analysis is suited for plant community data because it delivers multiple responses of non-independent variables at the same time (Anderson, 2001). We chose a two-way factorial PerMANOVA with month as the blocking variable and rooting as the grouping variable to investigate changes in plant communities over time.

In November 2013, feral swine re-rooted areas of native grassland pasture in our study. Previous observations in similar habitat demonstrated that feral swine preferred to root in areas where Carolina redroot had become established (Boughton and Boughton, 2014). We conducted a chi-square analysis to determine if plots in which Carolina redroot was the dominant species (>50% of total plant species cover) prior to the re-rooting event were re-rooted more than plots where it was not the dominant species (RStudio Version 0.98.1091).

2.4. Economic analyses

We calculated the economic cost to the livestock industry in south central Florida associated with loss of forage due to feral swine rooting. To estimate the proportion of area that was disturbed, we divided the rooted area by the total area of each pasture. We estimated rooted areas as the area which was mapped along transects. This estimate of rooting was a minimum estimate,

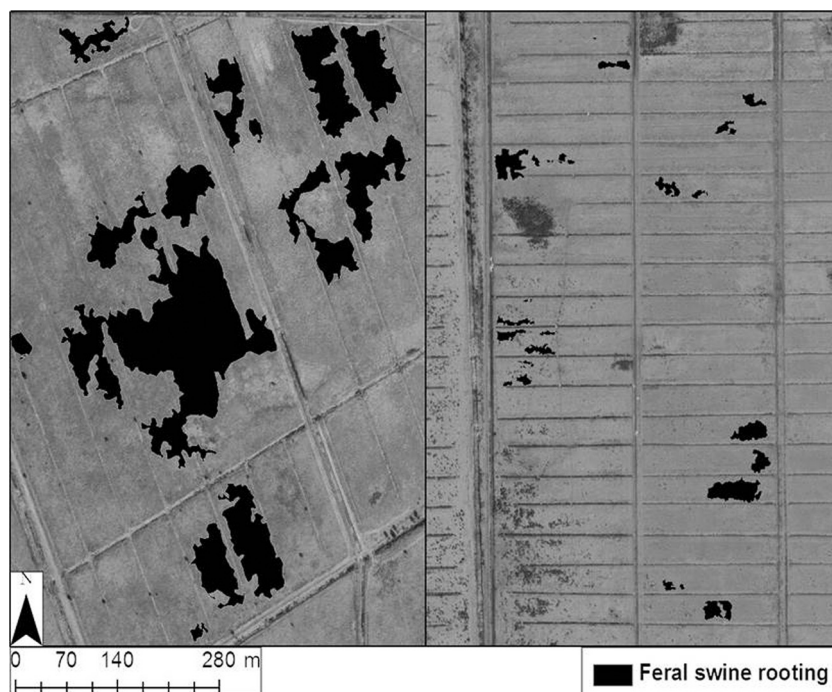


Fig. 1. Feral swine rooting (black polygons) in native grassland (left) in November 2013 was estimated to be 7.76 ha in 60 ha of pasture. Rooting on sown pastures (right) on MAERC in February 2013 was estimated to be 0.85 ha in 40 ha of pasture. Estimates of rooting were made from mapped rooted patches encountered while walking transects.

as the area only represents rooted patches that fell upon survey transects.

To determine forage loss within rooted areas, we classified each plant species as forage, unpalatable or unknown (Table 1) and compared the average cover of forage species monthly in each of the paired sets of sub-plots within each patch (4 rooted versus 4 un-rooted) for a total of 19 patch comparisons in native grasslands, and 8 in sown pastures. Because sown pastures and native grassland are utilized by Florida ranchers during different seasons: sown pasture in the summer growing season, and native grasslands as a standing hay crop during winter, we confined our estimation of potential forage losses to May through September for sown pasture (Newman et al., 2011), and October through February for native grassland. For each 5 month period, the amount of forage loss was averaged among subplot pairs.

To estimate the economic cost of forage loss, we modified a simple economic model based on the amount of beef, measured as calf weight, produced under realistic stocking densities per unit area (Ferrell et al., 2006). We assumed that forage was directly related to the ability of a unit area to produce beef and that any loss

in forage would cause a similar loss in beef production. The model was defined as:

$$\text{Calf kilograms produced per hectare} = \frac{W \times CW \times k}{R}$$

where, W is the weaning percent of a cow herd (we used the Florida average of 75%), CW = average calf weight (249.5 kg), k = rooting constant (value between 0 and 1 where 1 is equal to no rooting and 5% forage loss would be entered as 0.95), and R = stocking rate adjustment per hectare (we used 1 cow-calf pair per 1.2 ha for sown pasture and 1 cow-calf pair per 8 ha for native grassland). The calf weight was then valued at current market rates, ~\$5.68/kg during April 2015.

We extrapolated average forage grass loss due to rooting in both pasture types to a regional scale, including Highland County and the four adjacent counties: Okeechobee, Osceola, Polk, and Hardee. These five counties contained the highest density of cattle in the state of Florida and had extensive populations of feral swine. We summed the total amount of each pasture type regionally using the Florida Natural Areas Inventory (FNAI) Cooperative Land Cover

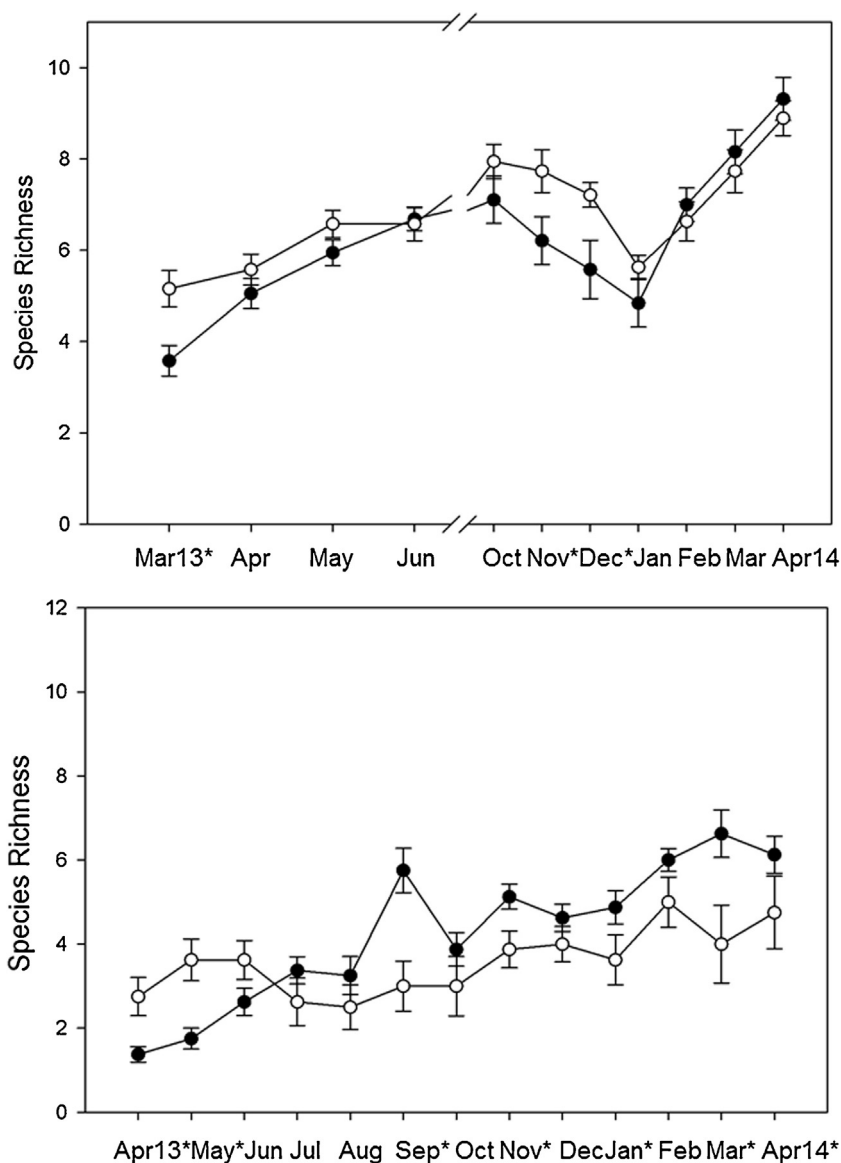


Fig. 2. Average species richness ± standard error in rooted (shaded) compared to unrooted (unshaded) patches in native grassland (top) and sown (bottom) pastures on MAERC as measured monthly in 2013 and 2014. Asterisked months indicate when species richness significantly differed among rooted and unrooted patches.

Map (v2.3, 2012), which contained improved and unimproved pasture as a land cover types with ArcMap (version 10.1). For sown pasture, we limited our estimates to sown pastures on soils found in our study to confine our inferences to similar plant communities in the region. These included the soil types Malabar fine sand, Felda fine sand, Pineda fine sand, and Tequesta muck as defined by NRCS Soils Map (2006).

3. Results

3.1. Mapped area of rooting

In native grassland pastures, the total area rooted along ten transect lines in February 2013 was 11,838 m². We mapped a total of 43 rooted patches, approximately four per transect, and the average patch size was 275 ± 98 m². The new rooting in November 2013 that bisected the original transects totaled 77,553 m², nearly a

sevenfold increase in less than a year (Fig. 1). Old and new rooted patches merged together in some areas, and the total number of rooted patches was condensed to 17, an average of about two per transect. The average rooted patch size increased to $4562 \pm 1,862$ m².

Rooted area in sown pastures along the eight transects totaled 8450 m². We recorded and mapped 29 rooted patches, an average of three per transect. Average patch size in these pastures was approximately 290 ± 284 m². We did not observe any re-rooting of these pastures. In total 13% (7.76 ha of 60 ha) of the native grassland pasture was rooted and 2% (0.85 ha of 40 ha) of the sown pasture was rooted.

3.2. Plant community diversity

Species richness in native grassland pastures differed in rooted versus unrooted patches, and depended on sampling month and

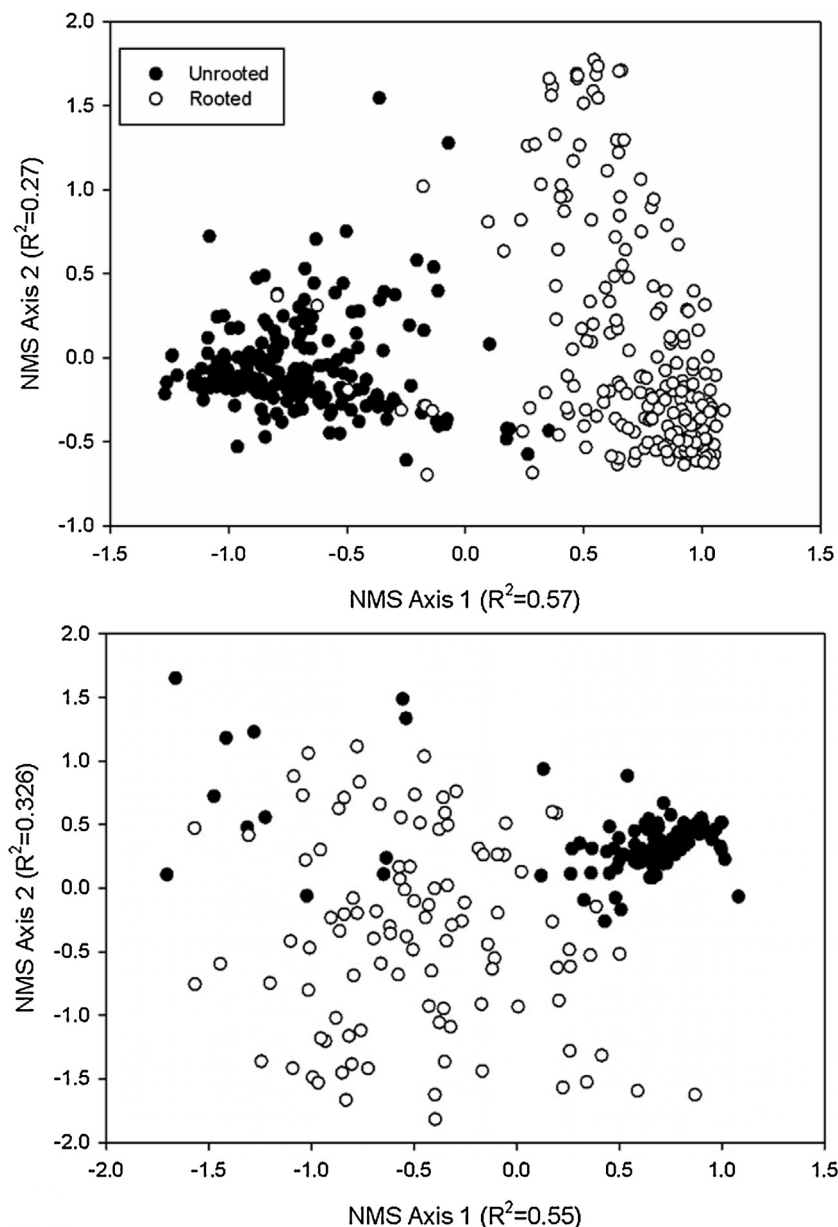


Fig. 3. Non-metric multidimensional scaling in native grassland (top) and sown (bottom) pastures comparing rooted (white circles) to unrooted (black circles) plant communities.

time since rooting ($df=10$, $F=4.19$, $p<0.001$). The number of unique species was significantly lower in rooted versus unrooted patches immediately following rooting events in February and November 2013, but was not significantly different in other sampling months (Fig. 2). In March 2013, richness in rooted patches was lower than richness in unrooted patches ($r=3.58 \pm 1.46$ vs. $u=5.16 \pm 1.74$, $p=0.003$). Following the re-rooting event in fall 2013, richness in rooted patches remained lower than in unrooted patches in November ($r=6.21 \pm 2.27$ vs. $u=7.74 \pm 2.05$, $p=0.004$) and December 2013 ($r=5.58 \pm 2.80$ vs. $u=7.21 \pm 1.18$, $p=0.002$).

In sown pastures, we found an overall trend of significantly different species richness among rooted and unrooted pastures among months ($df=12$, $F=7.12$, $p<0.001$). As in native grasslands, we found fewer plant species in rooted vs. unrooted patches in the two months immediately following the single rooting event in April (April 2013: $r=1.38 \pm 0.52$ vs. $u=2.75 \pm 1.28$, $p=0.003$; May 2013: $r=1.75 \pm 0.71$ vs. $u=3.63 \pm 1.41$, $p=0.004$). Unlike native grassland pastures, species richness in rooted patches on sown pasture surpassed that of unrooted patches and remained higher throughout the rest of the study. We found significantly greater species richness in rooted patches in September ($r=5.75 \pm 1.49$ vs. $u=3.00 \pm 1.69$, $p<0.001$), November 2013 ($r=5.13 \pm 0.83$ and $u=3.88 \pm 1.25$, $p=0.046$), January ($r=4.88 \pm 1.13$ vs. $u=3.63 \pm 1.69$, $p=0.046$), March ($r=6.63 \pm 1.60$ vs. $u=4.00 \pm 2.61$, $p<0.001$), and April ($r=6.13 \pm 1.25$ vs. $u=4.75 \pm 2.43$, $p=0.029$) 2014.

3.3. Plant community composition

The NMS ordination revealed different plant community compositions in rooted versus unrooted patches in native grassland pastures (Fig. 3). A three dimensional solution (final stress=9.55, final instability=0.00000, 103 iterations) was suggested, with all axes significantly contributing to the differentiation of communities ($p=0.004$). Axis 1 of the ordination ($R^2=0.57$) represented cover types that occurred more often in unrooted patches (low or negative values) or those that occurred less often in rooted patches (high, positive values) (Fig. 3). Axes 2 and 3 had low R^2 values ($R^2=0.27$ and $R^2=0.10$), therefore their interpretations were less clear, however correlation coefficients suggest they may be linked to sampling month or variation between replicated pastures. Carolina redroot showed a strong positive correlation ($r=0.501$) with Axis 1, as did bare ground and litter ($r=0.698$ and $r=0.747$, respectively). Broomsedge and panic grass showed strong negative relationships with Axis 1. Table 2 illustrates correlative relationships between all three NMS axes and all cover types. The non-parametric MANOVA confirmed that differences in plant community composition in rooted versus unrooted patches were significantly different depending on month ($df=10$, $F=7.30$, $p=0.0002$), and rooting contributed to nearly 61% of the variation in plant community composition within native grassland pastures.

In sown pastures, the NMS ordination revealed differentiation among plant communities in rooted versus unrooted patches (Fig. 3). A two dimensional ordination was suggested (final stress=14.96, final instability=0.000, 99 iterations), with both axes extracted by the NMS being stronger than expected by chance ($p<0.004$). Axis 1 represented the majority of the variation in plant community composition ($R^2=0.551$), and was interpreted as cover types that occurred more frequently in rooted patches (low or negative values) and those that occurred less frequently in unrooted patches (high, positive values). Bahia grass showed a very strong positive correlation with Axis 1 ($r=0.935$). Litter and bare ground showed high negative correlations with Axis 1 ($r=-0.654$ and $r=-0.684$ respectively). Sedges were negatively correlated with Axis 1 ($r=-0.256$). Table 3 illustrates correlative

Table 2

Pearson's correlation coefficient between NMS axes and plant species/cover types in native grassland pastures on MAERC. Bold values are significant at $P<0.05$.

Cover type	Axis 1	Axis 2	Axis 3
<i>A. fissifolius</i>	-0.245	-0.052	0.051
<i>P. longifolium</i> Torrey	-0.721	-0.263	-0.341
<i>S. bakeri</i>	-0.032	0.085	-0.303
<i>A. virginicus</i> L.	-0.848	-0.07	0.412
<i>P. hemitomom</i>	-0.023	0.137	-0.471
<i>C. dactylon</i>	0.052	0.025	0.087
<i>Cirsium</i> spp.	0.137	0.25	0.059
<i>Cyperus</i> spp.	-0.017	0.281	-0.221
<i>L. caroliniana</i>	0.501	0.737	-0.075
<i>E. capillifolium</i>	0.014	0.365	-0.031
<i>R. leucodermis</i>	-0.12	0.014	0.03
<i>B. mitis</i>	0.02	0.078	-0.328
<i>C. asiatica</i>	-0.271	0.064	-0.519
<i>D. virginiana</i>	0.093	0.016	-0.062
<i>H. umbellata</i>	0.018	0.068	-0.385
<i>J. angusta</i>	0.008	0.259	0.115
<i>L. repens</i>	0.07	0.085	-0.074
<i>Rhexia</i> spp.	0.002	0.296	-0.08
<i>B. caroliniana</i>	-0.125	0.006	-0.261
<i>E. minor</i>	-0.014	0.051	-0.034
<i>P. palustris</i>	-0.038	0.08	-0.337
<i>E. vivipara</i>	-0.075	0.04	-0.281
<i>Rhynchospora</i> spp.	-0.292	0.024	-0.137
<i>E. graminifolia</i>	-0.057	-0.029	-0.029
Bare ground	0.698	-0.387	0.235
Litter	0.747	-0.541	0.02
Water	0.034	0.628	0.284

relationships between both NMS axes and all cover types. The results of the non-parametric MANOVA confirmed that the plant communities in rooted versus unrooted patches were significantly different depending on month ($df=12$, $F=5.47$, $p=0.0002$) and that rooting contributed to nearly 48% of the variation.

In support of the hypothesis that feral swine seek areas dominated by Carolina redroot, we found that rerooted subplots were more likely to have been dominated (>50% cover) by Carolina redroot prior to rooting than not in native grasslands (Chi-squared=8.51, $df=1$, $p=0.003$) suggesting that feral swine preferred to root in areas with Carolina redroot. Ninety-one percent (58 of 64 subplots) of the re-rooted subplots were previously dominated by Carolina redroot in June 2013 compared

Table 3

Pearson's correlation coefficient between NMS axes and plant species/cover types in sown pastures on MAERC. Bold values are significant at $P<0.05$.

Cover type	Axis 1	Axis 2
<i>A. fissifolius</i>	-0.118	0.492
<i>S. bakeri</i>	0.054	-0.037
<i>A. virginicus</i>	0.059	0.076
<i>P. notatum</i>	0.935	-0.181
<i>C. dactylon</i>	-0.135	0.587
<i>Cirsium</i> spp.	-0.03	0.545
<i>Cyperus</i> spp.	-0.256	0.5
<i>S. indicus</i>	-0.082	0.3
<i>E. capillifolium</i>	0.026	0.445
<i>C. asiatica</i>	0.008	0.302
<i>D. virginiana</i>	-0.114	0.117
<i>H. umbellata</i>	0.096	-0.062
<i>L. octovalvis</i>	-0.116	0.042
<i>L. repens</i>	-0.128	0.118
<i>P. nodiflora</i>	-0.144	0.195
<i>Rhexia</i> spp.	0.012	-0.05
<i>E. vivipara</i>	-0.088	0.178
<i>Rhynchospora</i> spp.	-0.017	-0.07
Bare ground	-0.684	0.032
Litter	-0.654	-0.452
Water	-0.16	-0.539

to 60% (7 of 12) of the plots that were rerooted but did not have Carolina redroot as a dominant plant.

3.4. Forage grass economic analysis

In both pasture types, rooted subplots had less forage grass throughout the year compared to unrooted subplots (Fig. 4). During winter (October–February) when native grassland pastures were used for grazing, there was 53–68% less forage grass in rooted plots compared to unrooted plots. On average, 60% less forage grass was available over time in native grassland. In sown pastures, we found a decrease of 31% (February 2014, 10 months into the study) to 67% (May 2013, 2 months into the study) less Bahia grass in rooted plots compared to unrooted plots in sown pastures. In June, the most productive month for Bahia grass in terms of adding weight to cattle, there was 44% less Bahia grass cover per m² in rooted plots compared to unrooted plots. For the economic analysis, we used values of 60% and 44% forage loss in native grassland and sown pastures, respectively, that had been rooted.

In addition to estimating the amount of forage loss in rooted areas, we also estimated the extent of rooting in pastures. In our economic model, we varied the extent of rooted area from 2 to 30% for sown pasture (we estimated a minimum area of rooting in our study to be 2%) and 13 to 30% for native grassland pasture (based on our minimum estimate of 13%, Table 4). Based on our equation of beef produced per ha using baseline values for sown pasture (155.94 kg/ha) and no forage loss due to rooting, sown pasture yielded a value of \$885.10/ha. Applying a 44% loss within rooted area multiplied by a 2% area over which the pasture was rooted, we estimated a decline in production to 154.63 kg of beef/ha worth \$877.67/ha, for a loss of \$7.43/ha (Table 4). Extrapolated to 2225 ha of sown pasture, feral swine rooting would cost \$16,542/yr in lost beef production on MAERC. In the five county region the economic loss was estimated at >\$2.1 M annually. Using the same economic model using baseline values for native grassland pastures, we estimated that MAERC would lose \$8.28/yr/ha, or \$15,077 annually on its 1820 ha of native grassland pasture. Regionwide on similar

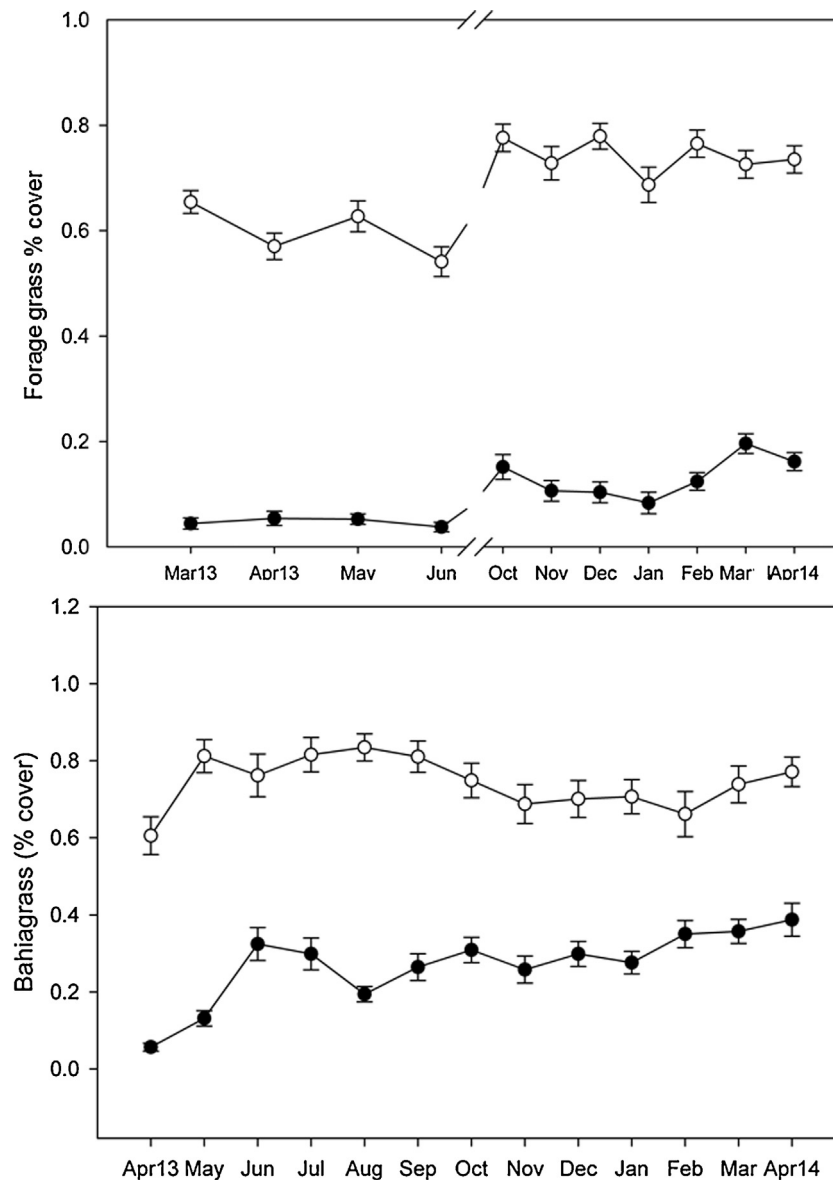


Fig. 4. Average percent cover of forage grass \pm standard error in subplots of rooted (shaded) areas compared to unrooted (unshaded) areas of native grassland (top) and sown (bottom) pastures on MAERC.

Table 4

Economic costs of forage loss calculated from estimated loss of kg of beef per ha due to decreased forage availability.

Pasture rooting	Calf beef production kg/ha	Calf beef value/ha	Cost of rooting/ha	Cost of rooting/acre	Regional cost
Sown no rooting	155.94	\$885.10	\$0.00	\$0.00	\$0
Sown w/2% rooting	154.63	\$877.67	\$7.43	\$3.01	\$2,160,568
Sown w/10% rooting	149.08	\$846.16	\$38.94	\$15.76	\$11,317,259
Sown w/20% rooting	142.22	\$807.21	\$77.89	\$31.52	\$22,634,517
Sown w/30% rooting	135.35	\$768.27	\$116.83	\$47.28	\$33,951,776
Native no rooting	18.71	\$106.21	\$0.00	\$0.00	\$0
Native w/13% rooting	17.25	\$97.93	\$8.28	\$3.35	\$190,545
Native w/20% rooting	16.47	\$93.47	\$12.75	\$5.16	\$293,146
Native w/30% rooting	15.34	\$87.09	\$19.12	\$7.74	\$439,718

soil types, we estimated that losses could exceed \$190,000/yr (Table 4).

4. Discussion

Feral swine are non-native ecosystem engineers that affect plant community dynamics through rooting activities. Rooting is an intense disturbance that can completely remove the above-ground vegetation (Cushman et al., 2004) and cause changes to soil properties (Aplet et al., 1991; Singer et al., 1984). We found that the trajectory of recovery for community diversity differed among pasture types; yet in both pasture types, community composition was altered after rooting. From conservation and agricultural production perspectives, rooting by feral swine had both ecological and economic consequences.

4.1. Ecological consequences of feral swine rooting

In native grassland pastures, recovery was a dynamic process that appeared to push the plant community into an alternate stable state. Immediately following the rooting event, diversity was greater in areas without rooting than areas which were rooted, but diversity recovered shortly thereafter. Although plant species diversity recovered after rooting disturbance, the plant community composition changed dramatically. In areas where rooting occurred, forbs and unpalatable species, plant litter, and bare ground dominated, while forage grasses, mainly broomsedge and panic grass, remained dominant in the unrooted subplots of native grassland pasture. Carolina redroot was the most abundant species in rooted areas, but dog fennel, buttonweed, and thistle were also more abundant in rooted than in unrooted areas. None of these species is palatable forage, and thistle is considered a weed and must be controlled with herbicides to maintain high forage quality. Intrusion of dog fennel is highly undesirable, because the plant can cause dehydration in cattle (Sellers and Ferrell, 2013). Dog fennel is ranked in the top three worst weeds for ranchers in this region, and if left unchecked causes forage grasses to decline through competition (Ferrell and MacDonald, 2005). Bare ground, which has been shown to hinder infiltration and increase runoff and erosion (McGinty et al., 1979; Self-Davis et al., 2003), also increased in rooted areas.

The dominance of Carolina redroot in rooted areas and the preference for feral swine to re-root in Carolina redroot patches supports the idea of a positive feedback loop between feral swine and Carolina redroot (Boughton and Boughton, 2014). Thus it appears that feral swine activity creates opportunity for expansion of a native invasive species. Similar to non-native invaders, native invaders may have adverse effects on certain ecosystems (Carey et al., 2012), and are often the result of anthropogenic disturbance (Simberloff et al., 2012). The mechanisms underlying this positive feedback are poorly understood, but could include either abiotic

(i.e., nutrient enhancement) or biotic changes (i.e., spreading root fragments) to the ecosystem. Carolina redroot and dog fennel have underground rhizomes in which nutrients are stored. In species with underground storage organs (i.e., bulbs), rooting by feral swine increases the nutrient content of these structures, which may favor the persistence and spread of these plants (Palacio et al., 2013). Although this study did not follow the fate of these habitat patches over multiple years, the plant species which recolonized rooted areas, namely Carolina redroot and dog fennel, have been shown to persist which may create an alternate stable state of community composition.

In sown pastures, we found that after rooted patches recovered from the initial rooting event, diversity was higher in these patches. This increase in diversity in rooted areas, however, equated to a loss of Bahia grass, a high quality forage that is established to increase cattle production. This result is similar to findings by Cushman et al. (2004), who observed an increase in plant species diversity, particularly due to an increase in non-native forbs, in a California grassland previously dominated by non-native grasses. In our study, sown pastures were mainly composed of Bahia grass, therefore rooting in these monoculture pastures created space for unpalatable, ruderal species, such as sedges (*Cyperus* spp.), which compete with desirable forage grasses for resources (Futch and Singh, 2000). In these pastures too, bare ground was a dominant cover type in rooted patches, which contributes to runoff and erosion.

4.2. Economic consequences of feral swine rooting

Central Florida rangeland is operated by ~16,000 producers, two-thirds of which are small family producers, although the majority of cattle belong to large commercial operations (Swain et al., 2013). Like most commodity-based economies, profit margins are slim and even small economic expenses can affect profitability. Both native grassland and sown pastures are important habitats for cattle ranches to remain economically viable in this region. Native grassland pastures provide a standing hay crop for cattle during the dry winter months when it is too dry, cold and day-length limited for Bahia grass growth. Yet sown pasture is essential for profitable cattle production because it provides high quality forage grass for cattle which allows for higher stocking densities. Our estimates of forage loss by feral swine suggest that 78 ha of native grassland pasture are lost per 1000 ha; and for sown pasture, 8 ha are lost per 1000 ha. In the five county region encompassing the rangelands of central Florida, we estimated a regional loss of >300,000 ha of pasture area (290,600 ha sown pasture, 29,161 ha native grassland) that amounted to >\$2 M in production losses (Table 4). This estimate likely undervalues the level of forage loss because it was based on minimum estimates of area rooted and does not reflect future projections of the dynamic nature of the 7-fold increase in rooting

that we documented on our plots in one year. Increased rooting and cumulative impacts of forage loss could quite easily reach much higher values with unchecked feral swine populations. For example 20% rooting of pastures would equate to >US\$22,000,000 (Table 4). Our cost estimate only reflects the simple loss of forage and does not include the cost of increased weed control of expanding Carolina redroot and dog fennel populations or the extra supplemental feed needed to offset the forage losses to maintain production. At some point losses in sown pastures may accumulate to the point that would require reestablishment, costing ~\$750/ha. Thus, actual losses could be as much as an order of magnitude greater and increase over time.

In addition to the ecosystem services that provide economic benefit to the regional economy, central Florida rangelands provide important conservation and cultural value to the region. Native grassland pastures provide habitat for game species production. In south central Florida, White-tailed deer (*Odocoileus virginianus*), Wild Turkey (*Meleagris gallopavo*), and Northern Bobwhite (*Colinus virginianus*) rely on grassland habitat for cover (Swain et al., 2013). This habitat also supports sensitive or threatened grassland birds like the Eastern Meadowlark (*Sturnella magna*), Loggerhead Shrike (*Lanius ludovicianus*), and Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*). The increase in monocultures of Carolina redroot has unknown consequences for game species and sensitive grassland birds, although there is some evidence that Carolina redroot seeds are an important food source for Sandhill Cranes (*Grus canadensis pratensis*; Valentine and Noble, 1970). Sown pastures support important resources for the Crested Caracara (*Caracara cheriway*) and also provide habitat for grassland birds (Eastern Meadowlark, Loggerhead Shrike, and Northern Bobwhite) (Morrison and Humphrey, 2001). Continued damage to these pastures by feral swine could contribute to a decline in available resources for many bird species.

5. Conclusions

We have shown that in the absence of control, rooting damage by feral swine poses both ecological and economic threats to the cattle industry. Because cattle ranching profits are marginal in the best of times, increased costs can quickly cause consequential economic losses. These losses imperil rangelands, their conservation value and the ecosystem services they provide because owners may be forced to convert rangeland to other uses with a higher profit margin such as residential or commercial development or row crop agriculture (Martinuzzi et al., 2015). For damage to be reduced, region-wide, consistent population control of feral swine must be embraced by ranch owners and operators, as well as by Florida policy makers, who have legislated the legal status of feral swine as livestock on private lands. This status allows owners and commercial live trappers to ship live feral swine from one private property to another. Transporting feral swine occurs regularly to facilitate hunting on private lands, including rangelands. Movement of feral swine, sold for \$30–40 a head, has exacerbated the rapid increase and high densities of feral swine in the region (Giuliano, 2010). Thus, restriction or elimination of transporting feral swine for release would be an effective first step toward reducing damage to rangelands. Deterrents, such as fencing, are not realistic measures to protect large rangelands from feral swine rooting as they are too costly to install and maintain. Recognizing that hunting feral swine is a widespread cultural activity in the southeastern United States, we do not advocate for reduced hunting opportunities. Aggressive control of feral swine will reduce, but not eradicate this species from the region and will continue to allow for hunting opportunities. Ultimately, effective, integrated long-term population

management will be essential to reduce the ecological and economic cost of feral swine to Florida rangelands.

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