



Experimental test of the impacts of feral hogs on forest dynamics and processes in the southeastern US

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ARTICLE INFO

Article history:

Received 22 November 2008

Received in revised form 24 March 2009

Accepted 30 March 2009

Keywords:

Big thicket

Biological invasions

Disturbance

Exclosures

Forest regeneration

Soil nitrogen

Seed predation

Sus scrofa

ABSTRACT

The foraging activities of nonindigenous feral hogs (*Sus scrofa*) create widespread, conspicuous soil disturbances. Hogs may impact forest regeneration dynamics through both direct effects, such as consumption of seeds, or indirectly via changes in disturbance frequency or intensity. Because they incorporate litter and live plant material into the soil, hogs may also influence ground cover and soil nutrient concentrations. We investigated the impacts of exotic feral hogs in a mixed pine-hardwood forest in the Big Thicket National Preserve (Texas, USA) where they are abundant. We established sixteen 10 m × 10 m plots and fenced eight of them to exclude feral hogs for 7 years. Excluding hogs increased the diversity of woody plants in the understory. Large seeded (>250 mg) species known to be preferred forage of feral hogs all responded positively to hog exclusion, thus consumption of *Carya* (hickory nuts), *Quercus* (acorns), and *Nyssa* seeds (tupelo) by hogs may be causing this pattern. The only exotic woody species, *Sapium sebiferum* (Chinese tallow tree), was more than twice as abundant with hogs present, perhaps as a response to increased disturbance. Hogs increased the amount of bare soil by decreasing the amounts of plant cover and surface litter. Plots with hogs present had lower soil C:N, possibly due to accelerated rates of nitrogen mineralization. These results demonstrate that hogs may influence future overstory composition and reduce tree diversity in this forest. Management of hogs may be desirable in this and other forests where large-seeded species are an important component of the ecosystem. Further, by accelerating litter breakdown and elevating nitrogen in the soil, hogs have the potential to impact local vegetation composition via nitrogen inputs as well.

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1. Introduction

The presence of exotic animals can impact the diversity and functioning of ecosystems. In some cases these differences may be due to unusual activities of exotic animals, for example, when browsing mammals have been introduced where none historically existed (goats on islands—Hamann, 2004; Campbell and Donlan, 2005; Carrion et al., 2007) or no similar species historically existed (ungulates in New Zealand—Husheer et al., 2005). However, the effects of exotic animals may sometimes be the same as the effects of unusually high abundances of native animals. Indeed, in many cases, the changes in plant community composition caused by high densities of exotic mammals are comparable to the changes caused by high densities of these animals in their native range or by high densities of native animals in the exotic mammals' introduced range. For instance, dense populations of white-tailed deer in

North America often have impacts similar to those in habitats where they are introduced and abundant (Cote et al., 2004). In general, animals that are more novel in their behaviors or life history traits are more likely to become abundant in their introduced ranges and have large impacts (Lodge, 1993; Mack et al., 2000).

Herbivorous animals may influence the diversity and functioning of ecosystems through a number of mechanisms. Perhaps the simplest is directly through selective feeding on the vegetation or seeds of different plant species. A classic example is the effect of selective browsing by moose on forest composition and soil properties in boreal forests in North America. Experimental exclosures showed changes in dominant plant types, vegetation architecture, productivity, litter dynamics, and nutrient cycling (McInnes et al., 1992; Pastor et al., 1993). Because seed predators feed selectively on different sizes of seeds, the composition of this animal community can also change the types of plants that dominate a local community (Heske et al., 1994; Mendoza and Dirzo, 2007). For animals that feed on both seeds and vegetative structures of plants, such as feral hogs or white tailed deer, both

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mechanisms may be important for influencing plant community composition (Cote et al., 2004). Finally, animals may impact the structure and functioning of ecosystems through activities other than feeding, such as by creating soil disturbances via below-ground foraging (Rogers et al., 2001), wallowing (Trager et al., 2004), gathering of vegetation for nests (Ickes et al., 2005), or engineering ecosystem level effects on hydrology (Anderson and Rosemond, 2007). Of course, some species may effect plant communities through more than one, or perhaps even all, of these mechanisms.

1.1. Focal species

Feral hogs (*Sus scrofa*) are an abundant exotic species throughout the world. Texas supports a large hog population with estimates as high as 2 million (Taylor, 2003; Mapston, 2004). Feral hogs eat crops, prey on small mammals and livestock, and compete with livestock for food (Adams et al., 2005). Rooting by feral hogs can also create conditions unfavorable to livestock by creating injury-causing troughs and mounds and by influencing the plant composition of rangeland through the destruction of forage grasses (Sweitzer and VanVure, 2002; Tierney and Cushman, 2006). Algae blooms, oxygen depletion, bank erosion and soured water have all been attributed to the wallowing behavior of feral hogs, reducing the availability of water sources for livestock and wildlife (Taylor, 2003). Feral hogs may also compete with the native wildlife, including the collared peccary, white-tailed deer, turkey, squirrels, and waterfowl, for food and territory (Ilse and Hellgren, 1995; Mapston, 2004). Hogs may also change plant community composition favoring exotics through disturbance (Cushman et al., 2004) and seed dispersal (Simberloff and VonHolle, 1999). They may also affect soil structure, soil nutrients, input of nutrients to streams, and stream invertebrates via their rooting, defecation, and urination (Singer et al., 1984; Kaller and Kelso, 2006).

Hogs are very selective in their choice of foraging areas, which limits the inferences that can be drawn from observational studies. For instance, it has been shown that hog foraging patterns vary with vegetation composition and/or soil moisture (e.g. Barrett, 1982; Ilse and Hellgren, 1995; Kotanen, 1995; Caley, 1997; Dexter, 1998; Gaines et al., 2005). Moreover, their choice of foraging areas and their diets change throughout the year, as well as with sex and reproductive condition (Kurz and Marchington, 1972; Baron, 1982; Dexter, 1999). This strong evidence that hogs are non-random in their habitat usage makes it problematic to quantify their effects on vegetation composition or soils from observational studies. Simply, if dominant vegetation and soil characteristics determine hog activity, then it is very difficult (if not impossible) to determine hog effects on plant species composition and soil variables by comparing areas in which their activities are frequent to those in which their activities are infrequent or absent.

Despite extensive documentation of hog disturbance in south-eastern US forests where feral hogs are very abundant (e.g. Bratton, 1974, 1975; Singer et al., 1984; Kaller and Kelso, 2006), we know of only one experiment using replicated exclosures in forests in North America, or any other introduced range of hogs, that exclude hogs without excluding all other large ungulates such as deer (Sweitzer and VanVure, 2002 present preliminary data). There are examples of replicated tall fences that exclude all large mammals (e.g. Royo and Carson, 2005), single unreplicated fenced areas (e.g. Katahira et al., 1993), two cases of replicated experimental hog exclosures in their native range (Ickes et al., 2001; Gomez and Hodar, 2008), and one replicated hog exclosure experiment in California grasslands (Cushman et al., 2004). We established a replicated hog exclosure experiment in an east Texas forest to examine the impacts of exotic feral hogs on forest dynamics and soil nutrients.

1.2. Predictions

Feral hogs will: (1) decrease the abundance of saplings of large-seeded tree species (such as hickory or oaks) by consuming their seeds; (2) increase the abundance of small-seeded trees by creating favorable soil conditions and reducing competition; (3) increase the mortality of saplings, especially that of smaller ones; (4) break up and incorporate litter into the soil and lower soil C:N ratios.

2. Methods

2.1. Study site

We conducted this study in the Big Thicket National Preserve (BTNP). It is located in east Texas, USA at the convergence of several ecosystem types and is extremely diverse, especially for vascular plants (Marks and Harcombe, 1975). Anecdotal reports are that feral hogs have been abundant in this region for more than a century with a long-standing tradition of free range hog ranching (Loughmiller and Loughmiller, 2002). BTNP is divided into a number of non-contiguous management units. Our experiment was conducted in the Lance Rosier unit, which is the largest unit (~10,000 hectares) and is located near Saratoga, Texas (N30.23942E, W94.48131E). The area in which our experiment was set up had a mature forest canopy dominated by oaks (especially *Quercus falcata* [red], *Q. laurifolia* [laurel], *Q. nigra* [water], and *Q. pagoda* [cherrybark]), gums (*Liquidambar styraciflua* [sweetgum], *Nyssa sylvatica* [blackgum]), magnolia (*Magnolia grandiflora*), and loblolly pine (*Pinus taeda*). Abundant shrubs and small trees were American holly (*Ilex opaca*), yaupon holly (*I. vomitoria*), deciduous holly (*I. decidua*), beautyberry (*Callicarpa americana*), and red bay (*Persea borbonia*). The only exotic tree or shrub present in the area where our experiment took place was Chinese tallow tree (*Sapium sebiferum* or *Triadica sebifera*).

2.2. Experiment details

In January 2001, we set up sixteen 10 m × 10 m plots spaced along a 600 m transect running parallel to, and approximately 100 m northeast of, Little Pine Island Bayou. This area is near the center of the unit and is ~4 km from the nearest paved road. After putting corner steel t-posts in each plot, we randomly assigned each plot to a treatment: fenced or control. The fenced plots were surrounded by 100 cm high woven wire livestock fencing (10 cm mesh at the top grading to 5 cm mesh at the bottom), mounted on an additional 8 steel t-posts (12 total per plot) with three strands of barbed wire at the top, middle and bottom. Control plots had only the corner fence posts.

The fence was likely too short to exclude white-tailed deer, which are common in this forest. Since the fence did not track the variations in the ground closely, relatively small animals such as snakes, rabbits, armadillos, possums, raccoons, and rodents were likely able to move under the fences and thus had access to these plots as well. Some also could likely pass through the coarse mesh. Since trees overhung the fences in many places and were close to the fence as well, climbing animals such as squirrels and bobcats would likely have been able to go over the fence. Other than hogs, the animals most likely to be excluded from fenced plots might have been coyotes and foxes but they may have been able to enter as well by jumping or climbing the fences. We never observed any signs of hogs (e.g. feces, rubs, bristles, ground disturbance) in fenced plots.

Throughout the experiment, we visited the exclosures a minimum of twice per year and repaired any damage to the fences from falling branches or trees as needed. The only time there was serious damage to the fences was due to Hurricane Rita in September 2005 (see below). The time from damage to complete

repair of the fences in that case was approximately one month. The fences were fully functional when we collected the last data used in this paper (late, 2007).

2.3. Data collection

In 2001 (year 1), we identified to species, tagged, mapped, and measured the dbh (diameter at breast height) of all of the trees and large saplings (those over 140 cm tall) in the plots. For saplings >50 cm tall but <140 cm tall, we measured height instead of dbh. These size categories are the same as those used by Harcombe and colleagues in their studies of long-term forest dynamics in the Big Thicket (Harcombe et al., 1999). In addition, we identified, tagged, and measured the dbh of all trees with a dbh >10 cm that were located within 5 m of each plot because they may have strongly influenced seed input and light availability in the plot.

We remeasured all plants and tagged any new saplings that met the 50 cm minimum height criterion in 2004 (year 4). For those saplings that had achieved a height of 140 cm since the previous survey, we recorded a dbh instead of a height. For those trees or saplings that had decreased to a height <140 cm we recorded a height instead of a dbh. If a previously tagged plant decreased to a height <50 cm, we recorded that height.

Hurricane Rita passed near the experiment in September 2005 (year 5). It knocked down many trees, removed the branches from many more, and stripped the tags from many of the plants. Tag loss was especially likely for the smaller plants, which had their tags wired on, compared to the larger trees that had their tags stapled on. We were able to determine the identities of all the trees and larger saplings based on tags and/or mapped locations to determine hurricane induced mortality. However, because our mapping was not sufficiently precise and small saplings sometimes were present at high densities of conspecifics we were not able to reliably determine mortality for many of the small saplings that lost their tags in the hurricane. Following the hurricane, we discontinued the tagged plant demographic data collection as the sapling record would not be continuous.

In 2007 (year 7), in lieu of the tagged plant protocol, we counted the number of woody plants between 50 cm and 140 cm high by species in an area determined by a pair of 2 m wide diagonal transects between the corners (a total of ~49 m²).

We estimated ground cover by functional group in 2004 (year 4), 2006 (year 6), and 2007 (year 7). Functional groups were: graminoids, forbs, woody plants, mosses, litter (litter visible on the soil surface), or bare ground (exposed mineral soil). In 2004, we collected data on five 0.25 m² quadrats (0.5 m × 0.5 m). In 2006 and 2007, we collected data on eight 0.25 m² quadrats. We do not report results for mosses as they were an extremely rare category and yielded data too sparse to analyze.

In 2004 (year 4), we collected five 25 cm deep, 2 cm diameter soil cores from each plot. Before pulling each core, we pushed aside the surface litter. These samples were dried, ground, combined in equal parts by weight to make a composite sample, and analyzed for %C and %N in an autoanalyzer (LeeMann Labs Inc. Elemental Analyzer, Model CE 440).

2.4. Analyses

We used ANOVA to examine whether basal area in year 1 or 4 or the decrease in basal area in year 5 (Hurricane Rita) depended on hog exclusion treatment.

We tested whether the percentage of plants that grew or died in each plot between years 1 and 4 depended on hog exclusion treatment using ANOVA. Because plants were measured for a dbh or height, but not both, we analyzed these two groups separately. If a plant had a height in year 1 and a dbh in year 4, it was treated as a

plant that grew in the analysis for plants with heights. We also examined the growth data by analyzing the magnitude of individual growth using an ANOVA with terms for treatment and plot nested in treatment and used partial difference tests of adjusted means to test for significant effects of treatment on growth. Finally, we used logistic regression to test whether the odds of death for small saplings (50–140 cm tall) depended on plot treatment, their height, and the interaction of these factors.

We calculated log odds ratios (Log[# in fenced plots/# in control plots]) to investigate which species might be driving this diversity pattern. We compared these species patterns of occurrence to a binomial distribution to examine which species had distributions that were most unlikely to have occurred by chance. Because our goal was only to quantify relative responses of species, we did not perform a multiple comparison correction.

We used a graphical examination to explore whether seed size or seed dispersal syndrome influenced the log odds ratio of occurring in fenced versus control plots. We obtained average seed mass data from the literature (Schopmeyer, 1974). Species were categorized into a primary dispersal syndrome: meteorochor (wind dispersed), nautochor (water dispersed), dysochor (scatter hoarding animals), or endozoochor (post-digestion animal dispersal). Some species such as *S. sebiferum* had multiple dispersal syndromes (endozoochor and nautochor) in which case we classified them as a single syndrome that was reported to be the most common one. We followed up this analysis with an ANOVA and a regression to examine the effect of dispersal syndrome and seed mass, respectively, on the percent of saplings in fenced plots for each species.

We used repeated measures ANOVA to examine the effect of hog exclusion on ground cover. We square root transformed data to more closely fit the assumptions of ANOVA. In this analysis there was a fixed effect of fence treatment with plot nested in treatment as the error term. The two factors which were repeated in time (year, year × treatment) were tested with year × plot (nested in treatment) as the error term. Plot (nested in treatment) and year × plot (nested in treatment) were tested with the residual error term. We used partial difference tests to compare cover within a functional group within a year between treatments. This is a more liberal test of significance than that used for the treatment term in the ANOVA because it does not use variance at the plot level as the error term. Because of this, adjusted means contrast tests in each year can be significant without the treatment main effect being significant in the more conservative ANOVA test.

We tested the effect of hog exclusion on soil C:N (year 4) and the abundance and species richness of woody plants (year 7) using ANOVA. For every analysis we checked that data met the assumptions of ANOVA. All analyses were done using SAS 9.1 (SAS Cary, NC).

3. Results

Basal area was always independent of fence treatment. Basal area at the start of the experiment was 1.181 ± 0.091 m²/ha (mean ± 1 S.E., $F_{1,14} = 0.03$, $P = 0.86$). In year 4, it had increased to 1.185 ± 0.089 m²/ha ($F_{1,14} = 0.03$, $P = 0.86$). Due to Hurricane Rita in year 5, it decreased on average by 13% to 1.063 ± 0.107 m²/ha but this decrease did not depend on treatment ($F_{1,14} = 0.60$, $P = 0.46$).

Hog exclusion increased the growth rates of small saplings between years 1 and 4. For plants with heights (i.e. 50–140 cm tall in year 1), 43.0% grew and 28.8% died in control plots versus 58.8% that grew and 28.1% that died in fenced plots. However, the probabilities of growth ($F_{1,14} = 1.11$, $P = 0.31$) or death ($F_{1,14} < 0.01$, $P = 0.96$) were both independent of treatment. The odds of dying did depend on height with taller saplings more likely to die in the interval from years 1 to 4 (Chi-square = 6.89, 1 df, $P < 0.05$) but the

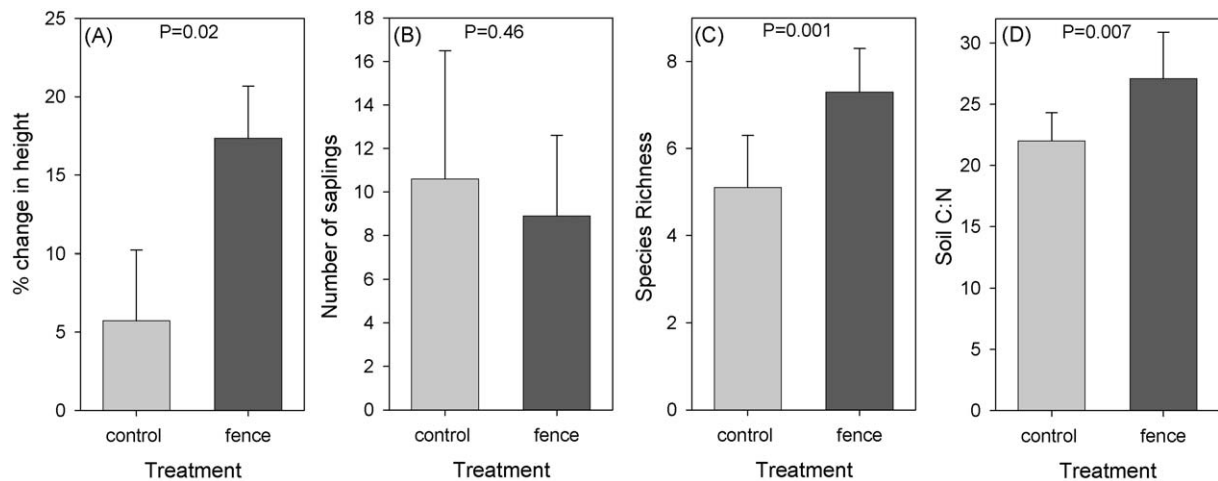


Fig. 1. Effect of hog exclusion by fences on (A) percent change in height of surviving saplings from 2001 (year 1) to 2004 (year 4), (B) number of saplings (50–140 cm tall) in 2007 (year 7), (C) species richness of saplings (50 cm to 140 cm tall) in 2007 (year 7), and (D) soil C:N in 2004 (year 4). All are means + 1 S.E.

effect of height on odds of dying did not vary with treatment (Chi-square = 0.16, 1 df, $P = 0.69$). However, for plants that survived, their change in height was significantly more positive in fenced plots compared to control plots (Fig. 1A, $F_{1,14} = 5.53$, $P = 0.04$).

Hog exclusion decreased survival of larger plants. For plants with a dbh (i.e. >140 cm tall in year 1), 62.2% grew and 1.9% died in control plots versus 58.2% that grew and 8.1% that died in fenced plots. This was not a significant pattern for growth ($F_{1,14} = 0.24$, $P = 0.63$) and dbh change of surviving plants was also independent of treatment ($F_{1,14} = 2.4$, $P = 0.14$). However, there was a significant difference in likelihood of death based on treatment ($F_{1,14} = 9.35$, $P < 0.01$). These deaths were *Q. nigra* (1 in control plot, 1 in fenced), *I. opaca* (1 in control), *I. decidua* (2 in a control), *Carpinus caroliniana* (3 in 3 fenced plots), *L. styraciflua* (2 in a fenced plot), *P. taeda* (1 in fenced), *Q. laurifolia* (1 in fenced), *N. sylvatica* (1 in fenced), and *Acer rubrum* L. (1 in fenced). Control plots had 0, 1 or 2 dead and fenced plots had 0, 1, 2 or 4 dead. We could not determine a cause of death for any individuals and all were standing dead.

Hog exclusion had no effect on the number of woody plants in year 7 (Fig. 1B, $F_{1,14} = 0.58$, $P = 0.46$) but it significantly increased their species richness (Fig. 1C, $F_{1,14} = 16.74$, $P = 0.001$). This pattern of higher species richness likely developed prior to the hurricane because there were 14 species represented in the new saplings added to the tagged survey in fenced plots in 2004 but only 6 species in the control plots.

Twelve species were found only in fenced plots with *P. taeda* and *Q. pagoda* the most unlikely to be distributed this way by chance due to their higher abundances (Fig. 2A). Eleven species occurred in both plot types but were more abundant in fenced plots with this unbalanced distribution least likely to have occurred by chance for *Q. falcata*, *I. decidua*, *A. rubrum* and *M. grandiflora*. Two species (*I. vomitoria* and *S. sebiferum*) occurred in both plot types but were more abundant in control plots and neither distribution was likely to have occurred by chance. Four species occurred only in control plots and this was least likely to have occurred by chance for *I. coriacea*.

Seed dispersal mode and size influenced the distribution of plants among fenced and unfenced plots but dispersal mode and seed size were strongly correlated. Dyschorous species that are dispersed by animals without gut passage and which all have large seeds in this forest (oaks and hickory) were all more likely to occur in fenced plots (Fig. 2B). There were no obvious patterns of distribution in fenced versus control plots for species that are wind/water dispersed (metoerchorous or nautochorous) or dispersed by animals with gut passage (endozoochorous). Dispersal mode was not a significant

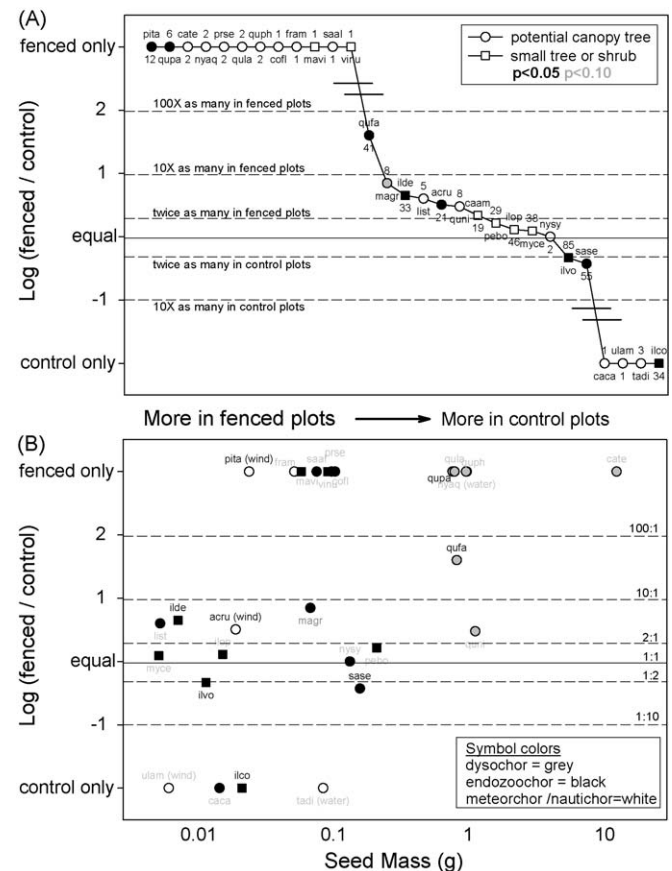


Fig. 2. Distribution of woody plants (50–140 cm tall) in control versus fenced hog exclusion plots. (A) Significance of woody plant species distributions compared to a binomial distribution. Numbers indicate the total number of individuals of each species. (B) Dependence of species distributions on seed size and dispersal syndrome. Species significant in part A is shown in black text in part B. Four letter codes indicate species: acru = *Acer rubrum* L., caam = *Calliandra americana* L., caca = *Carpinus caroliniana* Walt., cate = *Carya texana* Buckl., cofl = *Cornus florida* L., fram = *Fraxinus americana* L., ilco = *Ilex coriacea* (Pursh.) Chapm., ilde = *Ilex decidua* Walt., ilop = *Ilex opaca* Ait., ilvo = *Ilex vomitoria* Ait., list = *Liquidambar styraciflua* L., magr = *Magnolia grandiflora* L., mavi = *Magnolia virginiana* L., myce = *Myrica cerifera* L., nyaq = *Nyssa aquatica* L., nysy = *Nyssa sylvatica* Marsh., pebo = *Persea borbonia* (L.) Spreng., pita = *Pinus taeda* L., prse = *Prunus serotina* Ehrh., qufa = *Quercus falcata* Michx., qula = *Quercus laurifolia* Michx., quni = *Quercus nigra* L., qupa = *Quercus pagoda* Ell., quph = *Quercus phellos* L., saal = *Sassafras albidum* (Nutt.) Nees., sase = *Sapium sebiferum* (L.) Roxb., tadi = *Taxodium distichum* (L.) Rich., ulam = *Ulmus americana* Li. and vinu = *Viburnum nudum* L.

Table 1

Dependence of ground cover in plots on fence treatment (fence or control), year (years 4, 6 or 7), plot, and their interactions in a repeated measures ANOVA. Significant results are shown in bold. The difference in degrees of freedom for error reflects the distinct error terms for testing the effects of the fence treatment, year terms, and plot terms.

	df	Graminoid		Forb		Woody		Litter		Bare	
		F	P	F	P	F	P	F	P	F	P
Fence	1, 14	0.80	0.39	0.34	0.57	2.45	0.14	4.01	0.06	9.66	0.0077
Year	2, 28	15.30	0.0001	1.06	0.36	1.46	0.25	8.72	0.0011	0.06	0.94
Year × fence	2, 28	0.16	0.85	0.77	0.47	1.27	0.3	0.69	0.51	2.42	0.11
Plot	14, 288	16.00	0.0001	5.92	0	2.73	0.0008	20.13	0.0001	16.29	0.0001
Plot × year	28, 288	1.39	0.09	1.22	0.21	2.00	0.002	2.48	0.0001	1.83	0.0079

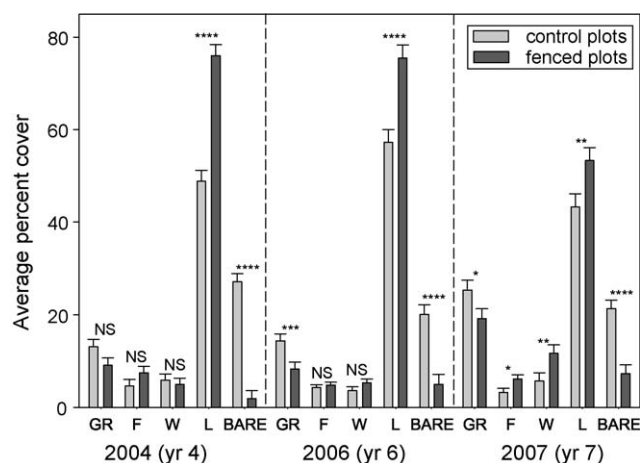


Fig. 3. Percent ground cover in control versus fenced hog exclusion plots. G = graminoid, F = forb, W = woody, L = litter on ground surface and bare = exposed mineral soil. Adjusted means and standard errors from repeated measures ANOVA (see Table 1). Numbers and symbols show significance levels in partial difference tests between treatments within a cover class and year.

predictor of percent of individuals within a species that occurred in fenced plots in an ANOVA ($F_{3,25} = 1.39$, $P = 0.27$). The percent of individuals occurring in fenced plots increased significantly with log seed mass in a regression (percent in fenced plots = $38.2 + 17.2 \times \log(\text{seed mass})$, $F_{1,27} = 6.11$, $P = 0.02$, $R^2 = 0.18$). Dispersal mode and seed mass were strongly related with dispersal mode predicting nearly two-thirds of the variance in seed mass (ANOVA $F_{3,25} = 13.96$, $P < 0.0001$, $R^2 = 0.63$, dysochorous > nautochorous > endozoochorous > metoerchorous).

Excluding hogs led to plots with on average less graminoid cover and bare ground but more forb cover, woody cover, and litter. Hog exclusion significantly reduced the amount of bare ground with the amount in fenced plots significantly lower than in control plots in each year (Fig. 3, Table 1). Litter and forb cover were on average higher, significantly so for litter in each year, and graminoid cover on average lower, in fenced plots every year (Fig. 3, Table 1). Litter and graminoid cover varied significantly among years with relatively more graminoid cover and relatively less litter in 2007 (Fig. 3, Table 1). Plots showed consistent cover patterns across years for each type of cover but some groups also varied among plots among years (Fig. 3, Table 1).

Soil C:N was lower in control plots than in fenced plots (Fig. 1D). This indicates that soil nitrogen levels were relatively higher in plots where hogs had access. This was driven more by reductions in soil percent nitrogen (control = 0.118 ± 0.022 ; fenced = 0.097 ± 0.015) than by changes in soil percent carbon (control = 2.69 ± 0.061 ; fenced = 2.64 ± 0.42).

4. Discussion

Excluding feral hogs from this forest in east Texas increased the diversity of woody plants in the understory, especially by

increasing the likelihood that those with large seeds would occur in a plot (Figs. 1C and 2B). Indeed, every species with an average seed mass >250 mg was more than twice as abundant in fenced plots as in unfenced plots (Fig. 2B). This strong signal for plants with this particular life history characteristic likely reflects the consumption of tupelo seeds (*Nyssa*), acorns (*Quercus*) and hickory nuts (*Carya*) by feral hogs in unfenced plots. Hogs are voracious consumers of Amast@ such as acorns and nuts (Wood and Roark, 1980) and they forage selectively in habitats where such foods are present (Baber and Coblenz, 1987). The positive impact of hog exclusion on diversity indicates that they are impacting the composition of the understory, and perhaps the future composition of the canopy, by their feeding on seeds.

4.1. Effects of feeding on seeds

A number of empirical studies and models have shown that seed predators may be strongly size selective and the composition of the granivorous animal community can have a strong effect on plant composition via selective predation on small versus large seeds (e.g. Tsujino and Yumoto, 2004; Mendoza and Dirzo, 2007). Two especially well known examples of this are tropical forests that have had their mammal fauna transformed by selective over hunting of large animal species that eat larger seeds (Wright et al., 2007) and long-term desert rodent exclosures in the southwest US in which exclusion of large granivores caused shifts in the plant community based on seed sizes (Heske et al., 1994). Since large-seeded species have been shown to be over-represented in the diets of feral hogs (Wood and Roark, 1980) and other studies have found negative correlations between hog rooting and oak regeneration in the native range (Bruinderink and Hazebroek, 1996; Gomez and Hodar, 2008), it is reasonable to conclude that large-seeded species are rare in control plots at least partly due to the direct effect of selective seed consumption by hogs.

However, there are a number of other reasons that woody plants with large seeds may be most impacted by the presence of hogs. First, dispersal mode and seed size were strongly correlated in this forest. All but one of the large-seeded species was dysochorous (*Quercus*, *Carya*) with the only exception being the water dispersed tupelo seeds (*Nyssa aquatica*) (Fig. 2B). Although seed mass was a better predictor of distribution among fenced versus control plots than was dispersal mode, it is still possible that dispersal mode and associated seed characteristics may be driving this pattern. For instance, it is reasonable that those species adapted to dispersal by gut passage are less affected by hog feeding though there is little information on the impact of hog gut passage on these particular species and there is some evidence that hogs have a larger than average impact on seed germination (Campos and Ojeda, 1996). Second, since seed number and seed size are often negatively correlated (Leishman, 2001), large-seeded species may be more sensitive to seed consumption simply because they are more limited by seed input in the absence of hogs. In other words, even if hogs consume similar proportions of large and small seeds, the impacts on sapling abundance may vary due to this

correlation of life history traits. Third, some other effect of hogs may be related to the success of large-seeded species, such as vulnerability to browsing or response to disturbance. However, there is no independent positive evidence of this.

4.2. Effects of feeding on plants

Hog exclusion increased the height growth rates of saplings (Fig. 1A). This is not an unusual or surprising result in that high densities of browsing mammals such as white-tailed deer may often reduce sapling growth rates (Cote et al., 2004; Long et al., 2007). One experimental study in the native range of hogs (Malaysia) also found increased sapling growth rates with hog exclusion (Ickes et al., 2001). It is interesting to note though that a number of studies have reported increased growth rates of trees in response to hog rooting in both the introduced range (Beech in Great Smoky Mountain Park—Lacki and Lancia, 1986) and native range (studies in Poland and Germany—reviewed by Lacki and Lancia, 1986). In some of those studies, authors have hypothesized this is a nutrient effect driven by increased available soil nitrogen (Singer et al., 1984; Lacki and Lancia, 1986).

Mortality rates of larger saplings were increased by hog exclusion. This was an unexpected result. The only study we are aware of that measured the effects of hogs on mortality of saplings directly was in the native range and hogs increased sapling mortality (Ickes et al., 2001). However, the total number of saplings that died was very small in our study and this result may indicate little about future overstory composition, *i.e.* a potential case of statistical but not ecological significance. In terms of a large effect on sapling numbers, we found no effect of hog exclusion on sapling abundance (Fig. 1B), which contrasts with the strong density effects seen by Ickes et al. (2001) in their enclosure study (though in that study hogs harvest saplings to build nests—a behavior never observed in North America). The mechanism proposed by others to explain positive effects of hog rooting on sapling growth rates, namely increased soil nutrients (Singer et al., 1984; Lacki and Lancia, 1986), could explain this positive effect of hogs on sapling survivorship as we observed increased soil C:N (*i.e.* relatively lower soil N) with hog exclusion (Fig. 1D). It is also possible that differences in intensity of competition for light contributed to these results. Overall, the effects of hogs on sapling abundance was minor and non-significant and the more conspicuous effect of hogs was in determining the species diversity and species composition of the understory (Figs. 1 and 2).

4.3. Indirect effects via disturbance

Hogs increased the amount of bare soil by decreasing the amounts of surface litter (Fig. 3). This almost certainly reflects the incorporation of this surface litter into the upper layers of the soil. Moreover, plots with hogs present had lower soil C:N possibly due to accelerated rates of nitrogen mineralization (Fig. 1D) which is consistent with more rapid integration of litter and surface soil. This is not a surprising result as increased soil nitrogen has been found in areas where hogs created extensive disturbances compared to areas that were not disturbed in other studies (Singer et al., 1984). Hog defecation and urination may also have contributed to relatively more nitrogen rich soils in plots where they had access (Frank and Evans, 1997). Other studies have linked hog disturbance with increased nitrogen in adjacent streams with effects on invertebrate and microbial communities (Singer et al., 1984; Kaller and Kelso, 2006). The high abundance of hogs adjacent to streams in the Big Thicket suggests that they may have similar effects in this region.

The relative abundance of different plant functional groups differed between fenced and unfenced plots with graminoids on

average more abundant in control plots and forbs and woody plants on average more abundant in fenced plots (Fig. 3). These effects were not significant across years but were significantly different within some years. Moreover, all vegetation combined was always far less than half the ground cover with litter and bare ground together always much more common.

The amount of ground disturbance caused by hogs in this study was high compared to other studies but typical, or perhaps low, for other areas in the Big Thicket. The amount of ground disturbance in control plots in this study averaged 22% of ground area across years (yearly average range 20–27%, Fig. 3). In a Rice University undergraduate lab survey of hog damage in the Turkey Creek unit of the Big Thicket in 2005, 40% of the ground surface had been turned over by hogs (unpublished data). A study conducted in 2004 found 21% of area of the Lance Rosier unit (the unit where this experiment took place), 34% of the area of the Big Sandy unit, and 27% of the area of the Turkey Creek unit had been disturbed by hogs (Chavarria et al., 2007). Neither of these studies was experimental and neither assessed the ecological impacts of the soil disturbance but merely quantified the amount of ground disturbance. Nonetheless, they suggest that our results may be conservative compared to the effects on forest regeneration or soil nutrients that would have been observed with hog exclusion in more heavily impacted units of the Big Thicket. However, compared to other published studies of feral hog disturbance, these amounts of soil disturbance are quite high (*e.g.* 7%—Kotanan, 1995) and our results may be more pronounced than would be expected with hog exclusion in other systems.

4.4. Local historical fauna

The impact of exotic animals on native plant communities is expected to be larger in communities where ecologically similar native animal species were absent (Hobbs and Huenneke, 1992; Strauss et al., 2006). For instance, the impact of feral hogs on native vegetation is large in Hawaii where plants have no evolutionary history with a large grubbing animal or a browsing mammal (Aplet et al., 1991; Katahira et al., 1993) but it apparently is minor in the Galapagos Islands where plants evolved with high densities of giant tortoises (Coblentz and Baber, 1987). Southeastern forests likely fall somewhere in between these two extremes. No native animals likely caused such extensive soil disturbances or would have been such voracious predators on large seeds in the southeastern US. It has been suggested that hogs are in some ways ecologically equivalent to omnivorous black bears (Kotanan, 1995) but we do not know of cases where bears create such widespread intense disturbances. Browsing mammals such as white-tailed deer are common. However, the impacts of high white-tailed deer abundances on oak regeneration observed in many US forested ecosystems (Cote et al., 2004) do not seem to occur in Big Thicket forests where deer populations are not unusually high and populations have not changed significantly in the last 25 years (Chavarria et al., 2006).

There are few predators currently present in east Texas forests that could limit the populations of hogs, though there were a number of predators when they were introduced in the 1600s. Historically, there were high abundances of black bears (*Ursus americanus*) but they have been locally extinct for nearly a century (Schmidly, 1994). Red wolves (*Canis rufus*) and Jaguars (*Panthera onca*) were probably never as abundant as bears but each is also absent from east Texas. Mountain lions (*Puma concolor*) are still present but very rare. Only the smallest carnivores such as bobcats (*Lynx rufus*) and coyotes (*Canis latrans*), which typically take only small piglets, are common. Alligators (*Alligator mississippiensis*) may kill some pigs. The largest sources of mortality of young feral hogs other than human hunters are thought to be starvation,

diseases, and parasites (Mapston, 2004). Density estimates from hunting success rates indicate that populations in the Big Thicket have doubled in the last 25 years (Chavarria et al., 2006).

It is possible that fences changed the foraging activities of other species. For instance, although animals such as white-tailed deer can easily jump over such short fences and squirrels can climb over or through them, they may have foraged less in fenced plots than in control plots. This could artificially increase the estimate of hog impacts and such a possibility cannot be excluded.

4.5. Effects on invasion

Hogs significantly increased the abundance of the only exotic woody species in our experiment, Chinese Tallow tree, with saplings of that species more than twice as abundant with hogs present compared to fenced plots (Asase et al. in Fig. 2A). This species is an aggressive invader of southeastern forests (Harcombe et al., 1999; Siemann and Rogers, 2003). It responds strongly to high light availability both in terms of survival and growth (Lin et al., 2004) so it is possible that hogs increased light availability and invasion, but this seems unlikely since they did not increase mortality of saplings or trees. Tallow trees also respond strongly and positively to increased nitrogen availability (Siemann and Rogers, 2007; Nijjer et al., 2008) so this may reflect a nutrient effect (Fig. 1D). Finally, even if tallow seeds have low viability after passage through hogs, hogs may increase local tallow seedling densities by dispersing seeds to places where they forage as is the case with *Opuntia* seeds invading olive groves (Gimeno and Vila, 2002). Regardless, given that both hogs and tallow tree are such aggressive invaders, the possibility of the invasion of one favoring that of the other is a significant concern (Simberloff, 2006).

5. Conclusions

Hogs may influence future overstory composition and reduce tree diversity in this forest directly through consumption of seeds, especially large dysochorous ones, and indirectly through soil disturbance. Management of hogs may be desirable in this and other forests where large-seeded species are an important component of the forest. Further, by accelerating litter breakdown and elevating nitrogen in the soil, hogs have the potential to not only impact local vegetation composition but also adjacent streams via nitrogen inputs and may promote invasion of Chinese tallow trees.

Acknowledgements

We thank: Candy Donahue, Maria Hartley, Rick Lankau, Danny Mee, Summer Nijjer, Dylan Siemann, and the Fall 2007 Bios 316 class (Rice University) for assistance; the Shell Center for Sustainability, Ford Foundation, Wray-Todd Fellowships and a Lodieska Stockbridge Vaughn Fellowship for support.

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