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Steven M. Gray

Gary J. Roloff

Daniel B. Kramer

Dwayne R. Etter

Kurt C. Vercauteren

*See next page for additional authors*

Authors
Steven M. Gray, Gary J. Roloff, Daniel B. Kramer, Dwayne R. Etter, Kurt C. Vercauteren, and Robert A. Montgomery

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*Research Article*

# Effects of Wild Pig Disturbance on Forest Vegetation and Soils

**STEVEN M. GRAY,**[1] *Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA*

**GARY J. ROLOFF,** *Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA*

**DANIEL B. KRAMER,** *Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA*

**DWAYNE R. ETTER,** *Michigan Department of Natural Resources—Wildlife Division, Lansing, MI 48911, USA*

**KURT C. VERCAUTEREN,** *National Wildlife Research Center, United States Department of Agriculture, Wildlife Services, Fort Collins, CO 80521, USA*

**ROBERT A. MONTGOMERY,** *Department of Fisheries and Wildlife, Michigan State University, 480 Wilson Road, 13 Natural Resources Building, East Lansing, MI 48824, USA*

**ABSTRACT** In North America, wild pigs (*Sus scrofa*; feral pigs, feral swine, wild boars) are a widespread exotic species capable of creating large-scale biotic and abiotic landscape perturbations. Quantification of wild pig environmental effects has been particularly problematic in northern climates, where they occur only recently as localized populations at low densities. Between 2016 and 2017, we assessed short-term (within ~2 yrs of disturbance) effects of a low-density wild pig population on forest features in the central Lower Peninsula of Michigan, USA. We identified 16 8-ha sites using global positioning system locations from 7 radio-collared wild pigs for sampling. Within each site, we conducted fine-scale assessments at 81 plots and quantified potential disturbance by wild pigs. We defined disturbance as exposure of overturned soil, often resulting from rooting behavior by wild pigs. We quantified ground cover of plants within paired 1-m$^2$ frames at each plot, determined effects to tree regeneration using point-centered quarter sampling, and collected soil cores from each plot. We observed less percent ground cover of native herbaceous plants and lower species diversity, particularly for plants with a coefficient of conservatism ≥5, in plots disturbed by wild pigs. We did not observe an increase in colonization of exotic plants following disturbance, though the observed prevalence of exotic plants was low. Wild pigs did not select for tree species when rooting, and we did not detect any differences in regeneration of light- and heavy-seeded tree species between disturbed or undisturbed plots. Magnesium and ammonium content in soils were lower in disturbed plots, suggesting soil disturbance accelerated leaching of macronutrients, potentially altering nitrogen transformation. Our study suggested that disturbances by wild pigs, even at low densities, alters short-term native herbaceous plant diversity and soil chemistry. Thus, small-scale exclusion of wild pigs from vulnerable and rare plant communities may be warranted. 

**KEY WORDS** disturbance, diversity, feral swine, invasive species, Michigan, regeneration, rooting, *Sus scrofa*.

Broadly, exotic species cause physical changes to biotic and abiotic components of an environment (Jones et al. 1994, 1997). Several classic examples exist for which exotic species have altered ecosystems. Gypsy moth (*Lymantria dispar dispar*) invasions in North America resulted in large-scale defoliation and changes to forest canopy structure (Fajvan and Wood 1996), releasing understory vegetation (Bell and Whitmore 1997), and subsequently increasing nest predation of forest-dwelling birds (Thurber et al. 1994). Invasion of North America and Europe by nutria (*Myocastor coypus*) corresponded with decreased diversity of emergent plants (Nyman et al. 1993), lower nest success of indigenous waterbirds (Angelici et al. 2012), and concomitant loss of wetland area (Boorman and Fuller 1981, Kinler et al. 1998, Carter et al. 1999).

Effects of exotic species are not always negative. In some instances, exotic species indirectly benefit ecological restoration (Ferrero-Serrano et al. 2011), and provide ecological services that may have been lost (Ewel and Putz 2004). In most systems within the non-native portion of the species' global range, wild pigs (*Sus scrofa*; feral swine, feral pigs, wild boars; Keiter et al. 2016) are detrimental to ecosystems because of their soil disturbance behaviors (Crooks 2002), which are primarily conducted when rooting for forage. For these reasons, large populations and high densities of wild pigs have potential to generate large-scale

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[1]*E-mail: stevenmgray4@gmail.com*

perturbations capable of altering biotic and physical components of a system (Bratton 1975, Singer et al. 1984, Arrington et al. 1999, Tierney and Cushman 2006). As omnivores and dietary generalists (Senior et al. 2016), wild pigs thrive in a variety of landscapes making them well-suited for invading new environments (Baskin and Danell 2003). When foraging, wild pigs use their spade-like snouts to overturn soil in search of roots, tubers, invertebrates, and other subterranean food.

Diets of wild pigs are predominately plant-based (Schley and Roper 2003, Ballari and Barrios-García 2014), though they also forage on a variety of vertebrates including amphibians and reptiles (Jolley et al. 2010), birds (Giménez-Anaya et al. 2008), small mammals (Wilcox and Van Vuren 2009), and carrion (Schley and Roper 2003, Turner et al. 2017). Consequently, high densities of wild pigs pose risks to native flora and fauna, potentially resulting in cascading effects to ecological communities and ecosystem function (Barrios-Garcia and Ballari 2012). The overall magnitude and influence of these effects will often vary by system and stage of the invasion process, meriting further exploration in newly colonized areas.

Wild pigs in the United States are responsible for an estimated $800 million in economic and ecological costs (Pimentel et al. 2005) and have been reported in 33 states as of 2018 (U.S. Department of Agriculture – Animal and Plant Health Inspection Service [USDA-APHIS] 2018). This distribution included localized populations that recently appeared beyond the bounds of natural range expansion, likely because of commercial hunting interests (Courchamp et al. 2003, Long 2003) and unlawful or unintentional introductions (Mayer 2009). This has resulted in emerging populations in northern portions of the United States that feature distinct vegetation communities, land cover types, and climates in comparison to other studied wild pig populations.

Michigan, USA, for example, is one of the states experiencing emerging wild pig populations, where the first recorded instance of a wild pig was in 1999 (Johnson v. Creagh, 12-50150-CZ, 2016). Since this event, sporadic reports have occurred indicating that wild pig populations occupy localized areas in the state at low densities (USDA-APHIS 2016). Though considered an invasive species throughout most of North America and in some locations naturalized (e.g., Southeast), in our study area we consider wild pigs as exotic given that populations in Michigan are characterized as emerging to transitional (Mayer 2009).

Though wild pigs alter ecosystems in other portions of their range (Singer et al. 1984, Arrington et al. 1999, Tierney and Cushman 2006), consequences of their disturbances are less understood in newly colonized ecosystems of the northern United States where this species occurs at low densities. Additionally, northern ecosystems in the range of wild pigs may be more susceptible to wild pig disturbance because no functional analog for this species existed historically. Thus, these areas provide a unique opportunity to assess the influence of wild pigs occurring at low densities, advancing understanding of the influence of wild pigs on northern ecosystems.

Wild pigs reduce plant cover (Singer et al. 1984, Rossell et al. 2016), plant species richness (Bratton 1975, Rossell et al. 2016), agricultural productivity (Bankovich et al. 2016), above-ground biomass (Ford and Grace 1998, Sweitzer and Van Vuren 2002), tree regeneration (Lipscomb 1989, Sweitzer and Van Vuren 2002), and ecosystem services (Pejchar and Mooney 2009). A potential outcome of wild pig disturbance is promoting establishment of other non-native species (Richardson et al. 2011). The mechanisms contributing to this pattern are unclear (Barrios-Garcia and Ballari 2012). Conversely, in some instances wild pigs positively influence plant species richness (Arrington et al. 1999) and growth (Lacki and Lancia 1986). Because of an increasing number of wild pig populations in northern climates of North America, information on direction, magnitude, and extent of environmental effects posed by this species is valuable for developing targeted management and conservation strategies in this region.

Our primary goal was to elucidate fine-scale spatio-temporal effects of wild pig disturbances to biotic and abiotic features to assess the influence of wild pig disturbance in northern ecosystems of the United States. Specifically, our objectives were to assess the effects of wild pig disturbances on ground-level plant communities, trees, and soil chemistry in forests of the central Lower Peninsula of Michigan.

## STUDY AREA

We conducted our study across 4 counties (Arenac, Bay, Gladwin, and Midland) in the central Lower Peninsula of Michigan between 2014 and 2016 (Fig. 1; ~6,102 $km^2$). Climate in this region is classified as humid continental with comparatively humid summers and cold winters. During our study, average monthly temperatures ranged from −6.5°C (Jan) to 20.8°C (Jul) with average monthly precipitation highest in September (8.9 cm) and lowest in February (3.9 cm; Michigan State Climatologist's Office 2017). Approximate annual seasons were spring (Mar–May), summer (Jun–Aug), fall (Sep–Nov), and winter (Dec–Feb). Our study area was located in the Saginaw Lowlands physiographic region, being relatively flat given its proximity to the coast (elevation range = 176–274 m; Lusch et al. 2009). Forests in the southern portion of our study area consisted primarily of deciduous hardwoods (e.g., maple [*Acer* spp.], poplar [*Populus* spp.], oak [*Quercus* spp.]), whereas northern counties (i.e., Arenac and Gladwin) included conifer (e.g., pine [*Pinus* spp.], fir [*Abies* spp.], spruce [*Picea* spp.]), mixed conifer, and hardwoods (Barnes and Wagner 1981, Albert 1995). Land cover in this region was primarily agriculture in the south with a higher prevalence of forestlands in the north and interspersed woody and emergent wetlands throughout. Most common mammalian fauna were white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), tree squirrels (*Sciurini* spp.), eastern cottontail (*Syvilagus floridanus*), and coyote (*Canis latrans*). Soil moisture regimes tended to be aquic (i.e., saturated for periods long enough to reduce oxygen) and udic (i.e., moist soils of humid climates that receive consistent rainfall; USDA

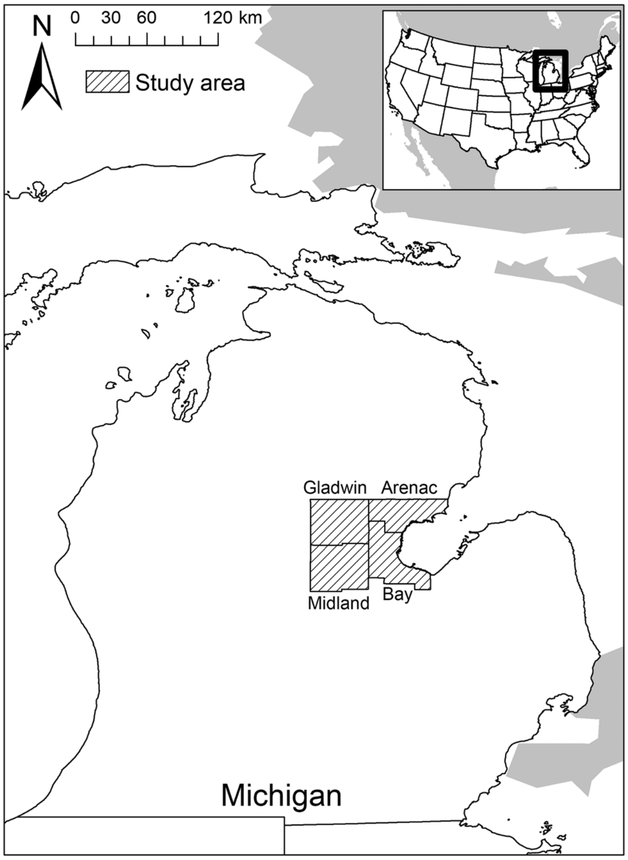


**Figure 1.** The 4-county (Arenac, Bay, Gladwin, Midland) study area in the central Lower Peninsula of Michigan, USA, 2016–2017.

Natural Resources Conservation Service [USDA-NRCS] 2018*a*), with soil temperatures ranging from mesic (i.e., 8–15°C) to frigid (<8°C; USDA-NRCS 2018*b*). We conducted research on state-owned lands managed by Michigan Department of Natural Resources and privately owned lands with landowner permission. Land use of these areas was primarily recreation, agriculture, and low to moderate development.

# METHODS

From 2014 to 2016, we captured and equipped 2 male and 5 female wild pigs with IridiumTrackM collars (Lotek Wireless, Newmarket, ON, Canada) in our study area. Of captured individuals, 5 (3 females, 2 males) were adults and 2 (females) were sub-adults based on size and weight. Given timing and location of captures, we inferred these individuals represented 3 separate groups occurring in our study area, but note wild pigs have a fission-fusion social structure where individuals readily change group membership (Ilse and Hellgren 1995, Gabor et al. 1999). After 3 years of monitoring (i.e., collecting and responding to public reports, remote camera surveys, aerial surveys) in collaboration with local management entities, we assumed that our sample of radio-collared individuals represented 20–30% of the population based on culling records and hunting forums. Furthermore, wild pigs have not occurred in the study area since 2018 (USDA-APHIS 2018). All capture and handling protocols were approved by the Michigan State University Institutional Animal Care and Use Committee (protocol number 01/14-013-00).

We programmed collars to record global positioning system (GPS) locations at 30-minute intervals, resulting in 22,172 GPS locations throughout our study area. Locations had a mean dilution of precision of $2.74 \pm 0.01$ [SE]). Bounded by the spatial extent of these locations, we overlaid a 285 × 285-m lattice (resolution = 8 ha) over the study area, and each cell of the lattice could serve as a potential sample area. We selected this resolution to approximate average patch size of forested vegetation and soil combinations in our study area (estimated to be ~11 ha). Within each cell we summed the number of GPS locations (range = 0–1,235) to serve as a proxy for intensity of use by wild pigs, where we hypothesized that cells with higher intensity of use would correspondingly contain greater amounts of disturbance by wild pigs. Here, we use the term disturbance to refer to a combination of behaviors performed by wild pigs that may disrupt the forest floor (e.g., rooting, wallowing, digging). When selecting sites, we stratified our sampling across various potential levels of disturbance intensity informed by the number of GPS locations within a cell. For biotic and abiotic assessments, we compared recently disturbed plots (<2.5 yrs) to plots without visual evidence of disturbance. This does not mean plots without visual evidence of disturbance were never disturbed by wild pigs. Given recent emergence of wild pigs in Michigan and observed low densities, however, we assumed historical instances of disturbance in these plots were negligible.

### Biotic Components

Within each 8-ha site, we surveyed a network of 9 240-m-long transects oriented in a north-south direction and spaced 30 m apart. We selected a 240-m transect distance because it represents the maximum length within each 8-ha site. Every 30 m along each transect we established a 2-m-radius plot, resulting in 81 sampling plots/site. We divided plots into 4 quarters, with each quarter serving as a sub-sample at the plot-level. In each quarter plot, we noted presence (1 = disturbed, 0 = undisturbed), intensity (depth below surrounding grade in cm), and percentage of wild pig disturbance. Field crews had experience differentiating wild pig disturbance (particularly rooting) from other potential sources of disturbance to the forest floor. In most instances, disturbance by wild pigs exceeded that of native fauna (e.g., raccoon, striped skunk [*Mephitis mephitis*], wild turkey [*Meleagris gallopavo*]) in both depth and surface area.

At every fourth plot within a site ($n = 20$), we randomly placed 2 1-m$^2$ Daubenmire frames (Daubenmire 1959) to measure vegetation coverage (%) of woody and herbaceous plants by species. We placed frames ≥1 m from plot center to ensure spatial separation between paired frames. We did not consider trees or shrubs ≥2 m in height to be part of the forest floor and we excluded them from our Daubenmire assessments. For plants not identifiable in the field, we recorded the finest level of taxonomy and photographed the specimen for later identification. Because of difficulty in differentiating among species of grasses and sedges, we broadly grouped these by family and did not seek finer taxonomic classification. In our second field season (2017), we revisited all sites and conducted vegetation assessments using the same transects and data collection protocol as in 2016. In 2017, however, we collected data only at paired disturbed and undisturbed plots not sampled in 2016 to broaden our characterization of the site and the temporal resolution of our data.

Because wild pigs frequently root near the base of trees (Sanguinetti and Kitzberger 2010), we examined relationships between wild pig disturbance and potential effects to various tree species. We considered any disturbance occurring near the stem of a tree (≥2 m in height) as potentially damaging because this could directly affect the root system. We used a point-centered quarter method (Cottam and Curtis 1956) at each plot (81/site) to characterize the tree community, and recorded evidence of disturbance within 2 m of the stem, tree species, and distance between each tree and plot center.

### Abiotic Components

We examined soil chemistry of paired disturbed and undisturbed plots within each site in 2017. We collected soils at ≥3 paired disturbed and undisturbed plots/site. For sites that were disturbed at >3 plots, we collected soil at 3 paired plots and every third plot thereafter. We stratified sampling within sites to account for soil type using the Soil Survey Geographic (SSURGO) database for soil classification (Soil Survey Staff 2016). At each location, we extracted 3 soil cores at a depth of 30.5 cm (diameter = 1.9 cm) and placed each sample into a plastic Ziploc® (S. C. Johnson and Son, Racine, WI, USA) bag for transport. In disturbed plots, we extracted samples directly from areas with overturned soil. We mixed samples obtained from the same site, disturbance (i.e., disturbed or undisturbed), and soil type combination in a plastic bucket to create a composite sample for testing. We used composite samples because we obtained more consistent laboratory results as the number of samples increased (Warncke 2000). We cleaned tools used for mixing samples between each use. We tested for pH and content of macronutrients (potassium, calcium, magnesium). In addition, we examined phosphorus using the Bray-1 extraction method (Bray and Kurtz 1945). For mineral nitrogen, we assessed ammonium and nitrate content of each sample. We selected these soil properties because they are readily quantified and the most likely to be influenced by wild pig disturbance. For example, disturbance by wild pigs has been indicated to alter nitrate concentrations and accelerate leaching of macronutrients (Singer et al. 1984, Mohr et al. 2005).

After collection, we promptly stored samples in a cooler and later transferred them to a freezer. We dried soil samples in an oven at 38°C and then finely ground and sieved (2 mm) each sample. We used soil-testing protocols designed and approved by the Michigan State University Soil and Plant Nutrient Laboratory (Brown 1998).

### Data Analysis

We explored relationships between prevalence and extent of disturbance and land cover classes using the 2011 National Land Cover Database (NLCD; Homer et al. 2015). We also extracted elevation, slope, drainage, and soil type from the SSURGO database for each of our plots. We estimated age of disturbance based on field notes and timestamps returned from GPS telemetry data. We selected the earliest occurrence within a site as the estimated date of disturbance, though we acknowledge that disturbances may have occurred later if wild pigs revisited a site. To examine effects of wild pig disturbance on forest floor plant communities, we ordinated plot-level percent cover of plant species using non-metric multi-dimensional scaling (NMDS) because this method allows for ordination of heterogeneous community data (McCune and Grace 2002). We implemented ordinations using the vegan package (Oksanen et al. 2019) developed for descriptive community ecology in R (version 3.5.0, R Foundation for Statistical Computing, Vienna, Austria). We initially conducted an ordination using all vegetation before parsing data by physiognomy, resulting in independent ordinations of woody and herbaceous vegetation. For each ordination, we maintained stress under a threshold of 0.15 because this level is considered reasonable for interpreting patterns in community data (Clarke 1993). To further explore separation of vegetation communities in ordination space, we applied a general additive model (GAM) using proportion of disturbance within a plot as an explanatory variable. We report the deviance explained and display resulting GAM contours within 2-dimensional ordination plots.

We tested for effects of wild pig disturbance on forest floor plant diversity in disturbed and undisturbed plots. We analyzed diversity of native plant cover, plants with a coefficient of conservatism ≥5 (Herman et al. 1997), and light- and heavy-seeded tree species. Species with a coefficient of conservatism ≥5 are considered obligates to natural areas, though these areas may not reflect pre-settlement conditions (i.e., are degraded; Herman et al. 1997). Light- and heavy-seeded tree species have different reproductive and germination strategies that can be affected by disturbances to the forest floor. Additionally, heavy-seeded tree species like oak and beech (*Fagus* spp.) provide mast that are food items for wild pigs (Henry and Conley 1972, Groot Bruinderink and Hazebroek 1995). We calculated Simpson's diversity index (Simpson 1949):

$$\lambda = 1 - \sum_{s} \frac{n_i(n_i - 1)}{N(N - 1)}$$

where, $n_i$ refers to percent cover of individuals belonging to the $i$th species and $N$ is the total percent cover of individuals of all species ($s$). Simpson's index was appropriate for our study because it is robust to small sample sizes (Lande et al. 2000). We calculated Simpson's diversity indices between disturbed and undisturbed plots within a site.

We implemented a use versus available resource selection framework (Manly et al. 2002), calculating a Manly selectivity index and chi-square analysis using the adehabitatHS package in R (Calenge 2019) to evaluate if wild pigs selectively rooted at the base of certain tree species. We plotted selection indices and confidence intervals for each tree species. In this case, larger selection ratio values with confidence intervals not overlapping 1 are indicative of selection, whereas smaller values falling below this threshold indicated avoidance. Tree species with confidence intervals that overlapped 1 were being selected proportionally to their availability (Desbiez et al. 2009). We used each plot within a site as a replicate, for 1,296 records.

For comparisons of plant diversity and soil characteristics between disturbed and undisturbed plots, we conducted a Welch's 2-sample *t*-test to explore whether these metrics differed by wild pig disturbance. We calculated Simpson's index at the site-level and displayed site-level diversity indexes by disturbance type using box and whisker plots. We also report the corresponding *P*-values and confidence intervals for each test.

## RESULTS

During the summers of 2016 and 2017, we conducted environmental assessments at 16 sites where we observed wild pig disturbance. In addition to mapping incidental field observations of rooting (confirmed by presence of tracks or scat), we used 19,867 locations from radio-collared wild pigs to determine site selection. Mean number of locations per individual wild pig was $3{,}167 \pm 271$. We collected locations across all seasons, but representation was greatest in fall (10,254), followed by winter (6,206), spring (3,055), and summer (352). The number of wild pig GPS locations within a site was not a reliable predictor of disturbance extent (Fig. 2). On average, $12 \pm 1.44\%$ of plots within a site were disturbed with a minimum of 2% and maximum of 21% (Fig. 2). The area disturbed within each plot ranged from localized patches $<1\,m^2$ to more expansive disturbance that encompassed the plot. Disturbance was relatively shallow, averaging $3.6 \pm 0.3$ cm, but we recorded depths of 28 cm. Disturbed plots occurred at an average elevation of $265 \pm 7.96$ m and slope of $3 \pm 0.22\%$. Within sites, wild pigs used deciduous forests when creating disturbance (63% used; 48% available), with woody wetlands being the second most commonly disturbed cover type (26% used; 41% available). Developed (e.g., urban, suburban), mixed forest, shrub and scrub, grassland, and emergent herbaceous covers were less common within sites (<3%), and we observed trace occurrences of disturbance in each (<1%). Plots were disturbed an estimated average of 584 days prior to sampling, with a minimum of 259 days and maximum of 853 days.

We conducted vegetation assessments at 320 plots in 2016 and 132 in 2017. We observed 155 plant species during our vegetation assessments. Common herbaceous plant species encountered in plots included grasses (Poaceae), sedges (Cyperaceae), wild lily-of-the-valley (*Maianthemum canadense*), bracken fern (*Pteridium aquilinum*), star-flower (*Trientalis borealis*), and sensitive fern (*Onoclea sensibilis*). We recorded a lower percent herbaceous plant ground cover in disturbed ($23.66\% \pm 0.95$) compared to undisturbed plots ($52.27\% \pm 0.54$).

Ordinations of percent ground cover of all plant species in disturbed and undisturbed plots displayed minimal separation between disturbed and undisturbed plots in ordination space (stress = 0.13; Fig. 3). Percent of the Daubenmire frame disturbed (explanatory variable) was responsible for 8.4% of the deviance explained. Hence, disturbance by wild pigs did not substantially influence overall plant community composition of the forest floor. Ordination of percent cover of woody plant species also revealed minimal separation between disturbed and undisturbed plots (stress = 0.14; Fig. 4), with the percent area disturbed explaining 2.8% deviance. Disturbance by wild pigs did not appear to influence the woody plant community of the forest floor. Conversely, herbaceous plant species showed distinct separation and clustering between disturbed and undisturbed

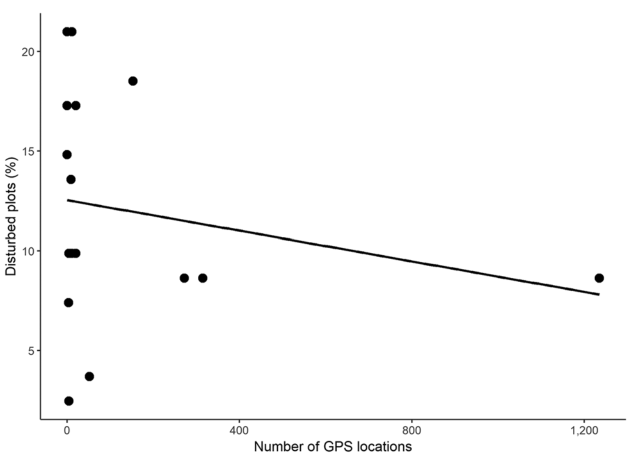


**Figure 2.** Relationship between disturbed plots (%) in an 8-ha site and number of wild pig global positioning system (GPS) locations for 16 sampled sites in the central Lower Peninsula of Michigan, USA, 2016–2017.

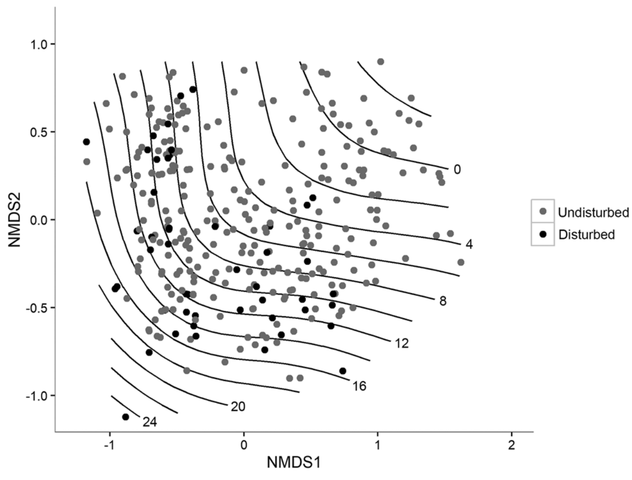


**Figure 3.** Non-metric multidimensional scaling (NMDS) of percent cover of forest floor plants in plots disturbed by wild pigs and undisturbed plots from 16 sampled sites in the central Lower Peninsula of Michigan, USA, 2016–2017. Contours depict the percent area disturbed within plots, used as the response variable in general additive modeling.

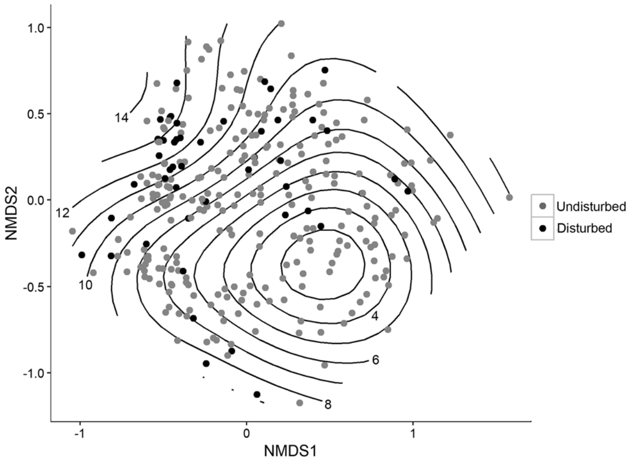


**Figure 4.** Non-metric multidimensional scaling (NMDS) of percent cover of woody vegetation communities in plots disturbed by wild pigs and undisturbed plots in 16 sites in the central Lower Peninsula of Michigan, USA, 2016–2017. Contours depict the percent area disturbed within plots, used as the response variable in general additive modeling.

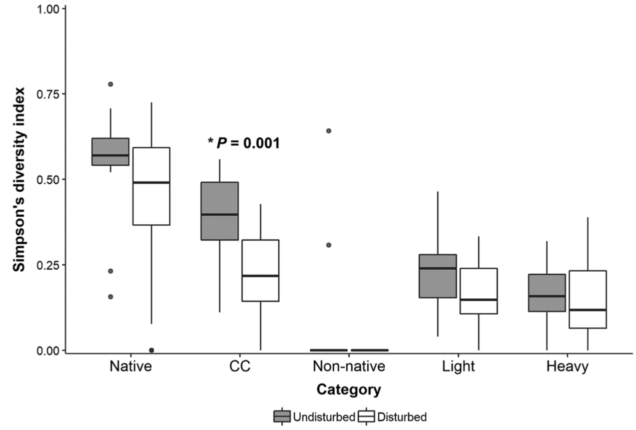


**Figure 6.** Site-level ($n = 16$) Simpson's diversity index in plots disturbed by wild pigs and undisturbed plots in the central Lower Peninsula of Michigan, USA, 2016–2017. Horizontal lines within boxes represent the median. Significant *P*-values from Welch's 2 sample *t*-tests are denoted by an asterisk. Native = native herbaceous plant species; CC = herbaceous species with a coefficient of conservatism ≥5; non-native = non-native herbaceous plant species; light = light-seeded tree species; heavy = heavy-seeded tree species.

plots (stress = 0.05; Fig. 5), and GAM modeling indicated percent area disturbed accounted for 73.6% of deviance explained.

Site-level Simpson's diversity index of native herbaceous vegetation cover was similar among undisturbed and disturbed plots ($P = 0.12$; Fig. 6). Contrastingly, diversity of herbaceous plant species cover with a coefficient of conservatism ≥5 was greater in undisturbed than disturbed plots ($P < 0.01$; Fig. 6). We failed to find enough non-native plant species to conduct a reliable comparison between disturbed and undisturbed plots (Fig. 6). Diversity of seedlings from light- and heavy-seeded tree species was generally higher for both reproductive strategies in undisturbed plots, but this difference was not statistically significant ($P = 0.09$, $P = 0.70$, respectively; Fig. 6).

We identified 336 individual trees and 24 species that had disturbance <2 m from the stem. We recorded wild pig disturbance most often near red maple (*A. rubrum*), white pine (*Pinus strobus*), and witch-hazel (*Hamamelis virginiana*), but specific tree species were not selected for (Fig. 7). Conversely, wild pigs avoided rooting near northern pin oak (*Q. ellipsoidalis*) and speckled alder (*Alnus incana rugosa*; Fig. 7).

We observed disturbance most often in soils considered sandy and moderately to poorly drained. The taxonomic order of soils most disturbed were Spodosols (rich in aluminum oxide and organic matter) followed by Entisols (undifferentiated mineral soils), with fewer occurrences in both Histosols (peaty soils, deep organic layer) and Mollisols (dark, humus rich surface layer with high calcium and magnesium). We collected 68 composite soil samples across 16 sites and 14 soil types. Welch's *t*-tests for group differences among soil characteristics in disturbed and undisturbed plots within a site did not yield significant

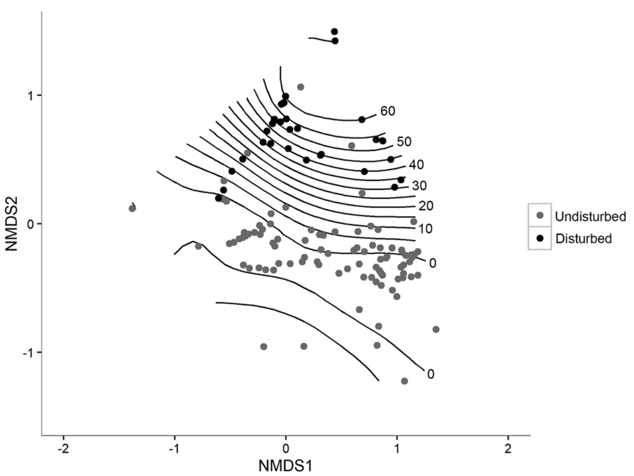


**Figure 5.** Non-metric multidimensional scaling (NMDS) of percent cover of herbaceous vegetation communities in plots disturbed by wild pigs and undisturbed plots in 16 sites in the central Lower Peninsula of Michigan, USA, 2016–2017. Contours depict percent area disturbed within plots, used as the response variable in general additive modeling.

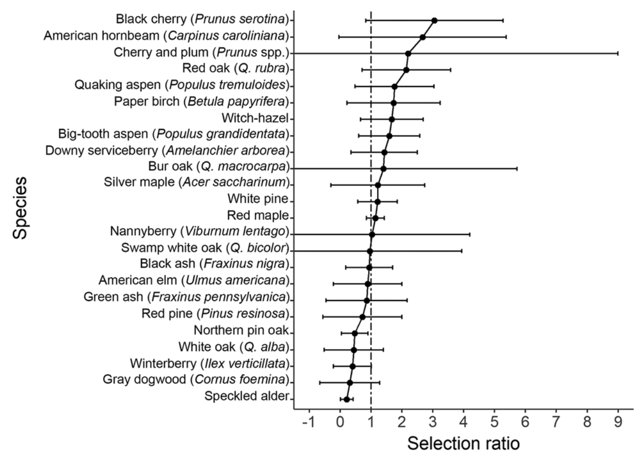


**Figure 7.** Manly selectivity index of wild pig disturbance and tree species in the central Lower Peninsula of Michigan, USA, 2016. Values to the right of the dashed vertical line indicate selection and values to the left indicate avoidance. Bars represent 95% confidence intervals.

**Table 1.** Mean and standard error (SE) of soil attributes in 8-ha plots that were disturbed by wild pigs or undisturbed in the central Lower Peninsula of Michigan, USA, 2016–2017.

| Soil attributes | Disturbed | SE | Undisturbed | SE | *P* |
|---|---|---|---|---|---|
| pH | 5.61 | 0.11 | 5.41 | 0.13 | 0.25 |
| Phosphorus (%) | 13.50 | 1.36 | 13.44 | 1.18 | 0.97 |
| Potassium (ppm[a]) | 47.59 | 2.19 | 52.32 | 2.51 | 0.16 |
| Calcium (ppm) | 865.09 | 149.69 | 1,289.12 | 176.14 | 0.07 |
| Magnesium (ppm) | 107.72 | 13.93 | 164.03 | 20.35 | 0.03[b] |
| Nitrate (ppm) | 7.53 | 0.91 | 8.00 | 0.86 | 0.71 |
| Ammonium (ppm) | 10.78 | 0.99 | 16.39 | 1.91 | 0.01[b] |

[a] Parts per million.
[b] Denotes significance at the 0.05 threshold.

differences in pH, phosphorus, potassium, or nitrate. Results for calcium were marginal ($P = 0.07$), with soils in undisturbed plots containing greater amounts of calcium. Similarly, soils in undisturbed plots contained significantly higher quantities of magnesium ($P = 0.03$) and ammonium ($P = 0.01$) than disturbed plots (Table 1).

## DISCUSSION

We explored effects of wild pig disturbances on environmental variables in the central Lower Peninsula of Michigan. Wild pigs altered structure and composition of herbaceous plant communities within approximately 2 years of forest floor disturbance. Wild pigs in the northern Michigan landscape create forest floor disturbances that exceed that of native fauna in depth and extent. The only comparable disturbances in this area could be attributed to humans (e.g., logging, agriculture). Although we did not record evidence that wild pig disturbances facilitated colonization of exotic species, we observed less cover of native herbaceous plants and lower diversity in disturbed plots, a trend particularly evident for plants of higher conservation value. Typical of a generalist, we did not detect evidence that wild pigs exhibited selection for specific tree species when rooting. We suspect that wild pigs were instead motivated by alternative sources of subterranean forage (e.g., invertebrates, fungi, seed middens; Focardi et al. 2000, Baubet et al. 2003, Gómez et al. 2003, Skewes et al. 2007). Although not significant, regeneration of light- and heavy-seeded tree species tended to be lower in disturbed plots. Concentrations of magnesium and ammonium were significantly lower in disturbed plots, suggesting that soil disturbances accelerated leaching of macronutrients, potentially altering nitrogen transformation processes. Collectively, our results indicated that wild pigs, even at low densities, have the capability to alter biotic and abiotic features in a landscape at fine spatio-temporal scales. Hence, even low-density wild pig populations may affect northern landscapes in the United States.

Disturbances by wild pigs affected herbaceous plants by reducing overall cover, consistent with other studies (Bratton 1975, Singer et al. 1984, Arrington et al. 1999, Cole et al. 2012, Cuevas et al. 2012). Disturbance by wild pigs also altered composition and structure of local herbaceous plant communities, apparently related to amount of disturbance within a plot. This aligns with previous research exploring effects of disturbance on plant communities in high-density wild pig areas including California (Cushman et al. 2004), Hawaii (Aplet et al. 1991), and the Great Smoky Mountains in Tennessee, USA (Bratton 1974). Furthermore, our plant diversity assessments indicated that wild pig disturbances significantly affected herbaceous species of high conservation value. These plants often depend on natural disturbances (e.g., tree fall gaps) or relatively undisturbed environmental conditions, and wild pig disturbances appeared to limit colonization and survival over the short term. Similar to our findings, effects to rarer plant communities by wild pigs has been documented in Hawaii (Loope and Madeiros 1994), and California (Santa Cruz Island; National Park Service 2002).

The structure and composition of woody plant species did not differ between disturbed and undisturbed plots. This result may be due to the relatively short duration of our study, which occurred over a span of about 2 years (from disturbance to field measurements). We expected to see increases in germination of light-seeded tree species in disturbed plots because rooting exposes mineral soils allowing for colonization. We also anticipated reduction in regeneration of heavy-seeded tree species in response to wild pig disturbance because mast from these species are important dietary components. In California, disturbance by wild pigs was reported to hinder oak regeneration through seed predation, and reductions in seedling size and survival (Sweitzer and Van Vuren 2002, 2008). Similar effects to regeneration of heavy-seeded tree species have also been reported in the native range of wild pigs (Groot Bruinderink and Hazebroek 1996, Gómez et al. 2003). Within 2 years of disturbance, there were slightly lower levels of tree regeneration for light- and heavy-seeded species in disturbed plots. Effects to tree regeneration appear to be more pronounced in areas with high-density wild pig populations (Sweitzer and Van Vuren 2002), potentially revealing why we did not observe stronger responses in our study.

Similar to other studies, we observed disturbances at or near the base of trees, which often exposed parts of the root system (Singer et al. 1984). Wild pig disturbances can expose root systems to drying, insects, or disease, potentially compromising tree vigor. Wild pigs did not select for tree species when rooting in Michigan. This result suggests that rooting behavior is not directly related to fruit or mast produced in the crown or canopy but rather some other form of subterranean forage, which is consistent with findings in beech forests of the Great Smoky Mountains (Bratton 1975). Potential alternative below-ground food sources influencing rooting behavior include fungi (Baubet et al. 2004, Skewes et al. 2007), invertebrates (Baubet et al. 2003), and small-mammal caches (Focardi et al. 2000, Gómez et al. 2003). We hypothesize that much of the intensive rooting observed directly at the base of trees was done to exploit small-mammal caches (Suselbeek et al. 2014) because deep excavations are often performed by wild pigs with the purpose of pilfering caches when other forage is scarce (Focardi et al. 2000).

We also found variation in the effects of wild pig disturbance on soil chemistry. Most notably, we observed a reduction in magnesium and ammonium in disturbed soils. Magnesium is essential for plant (Wilkinson et al. 1990), animal (Kruse et al. 1932), and microbial communities (Fulmer 1918). In plants, magnesium is primarily obtained from soils and is necessary for plant growth (Cakmak et al. 1994*a*, *b*; Cakmak and Yazici 2010) and protein synthesis (Cammarano et al. 1972, Sperrazza and Spremulli 1983). Magnesium also plays a role in plant immune systems and reduces tissue degradation by soft rotting pathogens (Huber and Jones 2013). Reduction of magnesium in soils following disturbance is expected because magnesium is readily leached through soil weathering (Mayland and Wilkinson 1989). Reductions in magnesium following wild pig disturbance were also observed in the Great Smoky Mountains (Singer et al. 1984).

Several studies have explored rooting effects to soil ammonium and have generally reported that levels of ammonium were similar in disturbed and undisturbed soils (Cushman et al. 2004, Siemann et al. 2009, Cuevas et al. 2012). We recorded less ammonium in disturbed soils in contrast to results found in the Great Smoky Mountains (Singer et al. 1984). Accumulation of ammonium in soils may arise under multiple conditions when nitrogen conversion is limited. Examples of these conditions include when soils have a lower pH, reduced oxygen, less organic material, limited soil moisture, or low temperatures (Mengel et al. 2001). Our findings suggest that disturbance by wild pigs may alter and potentially accelerate nitrogen transformation processes, although we would expect a concurrent change in nitrates, which we did not observe. We proffer that lower ammonium content in disturbed soils is a remnant of the physical disturbance to the ground layer, which aerates soils and alters soil temperature and moisture content.

We caution that our findings derive from relatively recent (within ~2 yrs) plant and soil responses to wild pig disturbances. The temporal window in this study provides insights on plant colonization, persistence through disturbance, effects on plant regeneration, and changes in soil chemistry while limiting other potentially confounding sources of disturbance. The overall direction and magnitude of environmental changes caused by wild pigs in northern systems of the United States was largely unknown. Some advocate for exploring potential roles and benefits of exotic species (Schlaepfer et al. 2011), with evidence pertinent to wild pigs (Gawel et al. 2018). Our results indicated that wild pigs affected herbaceous plant communities and chemical properties in soils. In our study, wild pig disturbance did not facilitate colonization of exotic plant species, as suggested by invasion complex theory (Richardson et al. 2011). Incidence of exotic plant species in our study was relatively low and effects of wild pig disturbance may be more pronounced in landscapes heavily dominated by exotic plants. Although the magnitude of some environmental effects we observed in this study were subtle, our results suggest that even at low densities and early in the invasion process, wild pigs have the ability to alter fine-scale biotic and abiotic components in northern systems.

## MANAGEMENT IMPLICATIONS

Given potential effects of wild pig disturbances to plant species, small-scale exclusion of wild pigs from rare or endemic plant communities may be warranted. Excluding wild pigs from these areas offers protection from direct disturbance to plants and indirect alteration to soil chemistry. Our study identified potential short-term effects from wild pig disturbances, suggesting that alterations to localized ecosystem dynamics may happen rapidly, necessitating expedient conservation action in areas featuring rare plant communities vulnerable to wild pig disturbances.

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