Accounting for heterogeneous invasion rates reveals management impacts on the spatial expansion of an invasive species

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Abstract. Success of large-scale control programs for established invasive species is challenging to evaluate because of spatial variability in expansion rates, management techniques, and the strength of management intensity. For a well-established invasive species in the spreading phase of invasion, a useful metric of impact is the magnitude by which control slows the rate of spatial spread. The prevention of spatial spreading likely results in substantial benefits in terms of ecosystem or economic damage that is prevented by an expanding invasive species. To understand how local management actions could impact the spatial spread of an established invasive species, we analyzed distribution and management data for feral swine across contiguous United States using occupancy analysis. We quantified changes in the rate of spatial expansion of feral swine and its relationship to local management actions. We found that after 4 yr of enhanced control, invasion probability decreased by 8% on average relative to pre-program rates. This decrease was as high as 15% on average in states with low-density populations of feral swine. The amount of decrease in invasion rate was attributed to removal intensity in neighboring counties and depended on the extent of neighboring counties with feral swine (spatial heterogeneity in local invasion pressure). Although we did not find a significant overall increase in the probability of elimination, increased elimination probability tended to occur in regions with low invasion pressure. Accounting for spatial heterogeneity in invasion pressure was important for quantifying management impacts (i.e., the relationship between management intensity and spatial spreading processes) because management impacts changed depending on the strength of invasion pressure from neighboring counties. Predicting reduction in spatial spread of an invasive species is an important first step in valuation of overall damage reduction for invasive species control programs by providing estimates of where a species may be, and thus which natural and agricultural resources would be affected, if the control program had not been operating. For minimizing losses from spatial expansion of an invasive species, our framework can be used for adaptive resource prioritization to areas where spatial expansion and underlying damage potential are concurrently highest.

Key words: control; elimination; expansion; invasion rate; invasive species; management; spatial heterogeneity; spatial spread; *Sus scrofa;* wild pig.

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Introduction

Approximately one-sixth of the land surface globally is in danger of being invaded by non-native species that can cause devastating perturbations to local ecosystems and human livelihoods (Early et al. 2016). The invasion process can be challenging to predict once a species becomes established and enters the spreading phase. The spreading phase for most invasions is driven by both short- and long-range dispersal (Shigesada et al. 1995). Invasion rate is slower initially and dominated by short-range dispersal, but increases over time, partly due to increases in long-range dispersal and establishment and growth of satellite populations (Andow et al. 1990). In some cases, long-distance dispersal can be human driven (Tabak et al. 2017, including illegal movements), making it challenging to predict spatial spreading patterns using mechanistic models that are informed by demographic processes of the invasive species and landscape alone (i.e., without data that describe anthropogenic movements). Thus, considering spatial heterogeneity in expansion rates is essential for understanding and predicting invasion rates, for planning effective spatial prioritization of limited management resources, and for evaluating the impacts of local management on global invasion rates.

Once established on continental mainlands, control of invasive species is logistically challenging and expensive because the containment of spatial spread is more difficult relative to confined local or island systems. Funders and the public can become unsupportive of expensive control programs for invasive species if clear evidence and metrics of progress are not presented routinely (Hone et al. 2017). In addition to providing justification of return on investment, developing practical evaluation frameworks that are applied from the beginning of large-scale control programs is also important for guiding control efficiently as conditions change (Elliott and Kemp 2016, Hone et al. 2017). Despite their importance, the development of comprehensive methods of evaluating the impacts of control measures on invasive species populations is underemphasized relative to other steps in the management process (Hone et al. 2017). Consequently, it remains challenging to plan invasive species programs that operate through local control efforts to collectively affect continental-scale invasion processes.

Even for local-scale management programs, monitoring progress and determining when objectives have been achieved are a major challenge (Morrison et al. 2007, Ramsey et al. 2009). Compared with local programs, invasive species management programs with large geographic extents present additional challenges. There are often limited or no pre-program data covering the extent of the geographic area to be managed. Secondly, because funding is distributed over relatively large spatial areas, funding to measure program outcomes in addition to conducting control operations may be limited. Thirdly, there are often cultural differences across large geographic areas such that stakeholder interests are in conflict, which can prevent implementation of program objectives and measures of outcome over the full geographic scope of interest (Decker and Chase 1997). And lastly, the outcome of interest can be difficult to measure with a single metric because both the program objectives and the damage caused by the invasive species can vary widely across space and time. Thus, it is important to develop multiple straightforward, sound metrics for assessing program progress that can infer the effects of management broadly without comprehensive sampling, while accounting for spatial heterogeneity in spreading processes.

To address gaps with evaluation methodologies for large-scale invasive species control programs, our first objective was to identify how funding a national-scale program can influence effort and patterns of control of an invasive species geographically through time. Understanding how funding for invasive species management can translate to realized management actions provides a foundation for designing research to assess cost-effectiveness, develop adaptive management tools, and evaluate the impacts of different management strategies. Our second objective was to evaluate the impact of local-scale management actions on national-scale rates of spatial spread of an invasive species. We also quantified the relationship between changes in the rate of spatial spread and factors such as management intensity, invasion pressure (occupancy status of neighboring areas), and funding levels. We hypothesized that the effects of management intensity would depend on the strength of invasion pressure. Our analysis provides a unique opportunity to understand the spatio-temporal impacts of large-scale invasive species programs on spatial invasion processes because national-scale databases for both control efforts and species distributions are rare. Such data are critical for developing monitoring plans and program assessment methods that can be easily applied to other invasive species systems. Our approach for determining spatial prioritization of future control work and fiscal resources over large geographic extents is relevant to a wide diversity of invasive species.

Materials and Methods

Study system

The recently established U.S. National Feral Swine Damage Management Program (NFSP), implemented in fiscal year 2014 by the United States Department of Agriculture/Animal and Plant Inspection Service (USDA/APHIS), is an example of a large-scale national invasive species control program. Feral swine (*Sus scrofa* or wild pigs, Keiter et al. 2016) have been expanding rapidly in the United States (Snow et al. 2017*a*) and are invasive species in the Americas, Oceania, and Australia, where they cause significant damage to native ecosystems (Hone 2002, Felix et al. 2014, Bankovich et al. 2016, McClure et al. 2018) and pose a health risk to wildlife, humans, and livestock (Miller et al. 2017). Even in much of their native range in Eurasia and Africa, they are often considered pests due to ecosystem disturbance from rooting behavior, predation of sensitive species, and disease threats to sensitive species, livestock, and humans (Massei and Genov 2004, Barrios-Garcia and Ballari 2012). Their high fecundity, generalist behavior, and ability to spread rapidly in new areas (Bieber and Ruf 2005, Massei et al. 2015) have presented an urgency to develop national-level control programs, especially in countries where they are non-native.

The objectives of NFSP are to eliminate feral swine populations in U.S. states where possible and reduce damage and disease risks where large populations are well established. Although the main motivation of NFSP is to protect human livelihoods (agriculture), and animal/human health, protecting native species and habitats of conservation concern is also paramount (e.g., Barrios-Garcia and Ballari 2012, McClure et al. 2018). The NFSP is implemented through state-level management activities and their cooperators (i.e., locally) which results in state-to-state variation in how objectives are implemented. Similarly, there is also variation in the amount of control that is implemented by cooperators (some of which is not recorded), making it impossible to attribute all effects to NFSP funding alone. Developing an evaluation method that accounts for regional heterogeneity in management intensity and rates of spatial expansion provides a unique opportunity for understanding the impacts of local-scale invasive species management programs at the national scale.

The impact of national-scale control programs for invasive species can be valued through two main metrics that comprise overall impact: reduction in damage or conflict in areas where the invader currently occurs, and prevention of further invasion and damage or conflict in new areas. Here, we focus on methods of estimating prevention of spatial spread of feral swine—a necessary component for estimating the value of ecosystem or economic damage prevented by nation-wide control efforts. We use two databases to evaluate changes that have occurred since the start of the NFSP: (1) the USDA/APHIS Management Information System (MIS) and (2) the National Feral Swine Mapping System (NFSMS). MIS records all wildlife management activities conducted by USDA/APHIS Wildlife Services (WS). NFSMS records spatial locations of feral swine sightings annually in all states, providing a temporally varying distribution of feral swine in the contiguous United States (see McClure et al. 2015, Snow et al. 2017*a* for predictive mapping with these data).

MIS database and processing

All database processing was conducted in R programming language (R Core Team 2016). The MIS data maintain WS control activities at the property level. Most of this work is funded by the NFSP, but some WS work is funded by other National, state, or local cooperators. We limited the MIS data to properties with feral swine removals and to properties with agreements in place to conduct removals of feral swine. For properties with feral swine removals, these data included the date/time, location (to the county level), methods of removal used (e.g., aerial gunning, ground shooting, traps, or snares), amount of effort relative to each removal method (e.g., number of hours flown in a helicopter, number hours spent ground shooting, or number of trap nights for traps or snares), and the number of feral swine removed by each method. We summarized spatial and temporal trends in the use of removal methods, counts of feral swine removed, effectiveness of each method, and the times and materials used by each method.

NFSMS database and processing

National Feral Swine Mapping System is maintained by Southeastern Cooperative Wildlife Disease Study (SCWDS) in collaboration with WS and University of Georgia (Corn and Jordan 2017). The data describe the distribution of feral swine across the conterminous United States annually since 2008. These data consist of polygons describing the known geographic extent of established feral swine populations that have been present for two or more years and have evidence of reproduction. Data are reported nationally from wildlife professionals from state wildlife resources agencies and WS via manual drawing of polygons that reference areas where feral swine meeting the mapping criteria have been observed. The general public is also part of the detection process as they regularly report sightings of feral swine which are then verified by state and Federal wildlife professionals by site visits and camera traps or removal methods. As feral swine are pests that cause obvious and often extensive damage to agriculture and other anthropogenic food sources, and because they are sought out by recreational hunters, there are many stakeholders that are monitoring for their presence.

We aggregated the NFSMS polygon data for each year from 2010 to 2017 to the county level. If a county had any overlap with a feral swine occurrence polygon, it was given a 1 (feral swine presence), otherwise it was a 0 (feral swine absence). We chose counties as our sampling unit because they represented the smallest common unit of measure for the MIS and NFSMS data. County size, of course, is variable across the United States (the mean is 2463 km^2 ± 95%, confidence intervals of 119 km^2, and a SD of 3375 km^2).

Maps of MIS removal data overlaid on NFSMS distribution data

We mapped the annual removal of feral swine (using MIS data) overlaid onto NFSMS reporting of feral swine presence. We aggregated both the removal and coverage data into 3 two-year time periods: 2012–2013 (prior to the start of NFSP), 2014–2015 (first two years of NFSP), and 2016–2017 (second two years of NFSP). Counties with no feral swine reported during the two years were 0, and counties with feral swine reported during at least one of the two years were 1 s. We used a two-year scale because although the NFSMS database was updated annually, the reporting system required that new populations be detected in a county for two years before it was considered occupied. To aid in visual interpretation (county boundaries were too small to distinguish colors), we aggregated data to Agricultural Statistics Districts (ASD; National Agricultural Statistics Service 2018) and classified the quantiles of these rates with separate color scales for areas within versus outside the distribution of feral swine (as determined by the NFSMS distribution data).

Analysis of removal patterns

To assess trends in removal over time, we fit a linear model with the log of county-level mean annual removal as the dependent variable, and the interaction of time period (2012–2013, 2014–2015, and 2016–2017) and state name as independent variables. We excluded states with less than 10 feral swine removal events over all counties and time periods. A negative coefficient for removal over time indicated less removal over time, potentially indicating that populations were being reduced (i.e., more difficult to find animals). In contrast, a positive relationship indicated more removals over time (i.e., more resources led to more removals) suggesting that population abundance was not yet affected significantly at the state level.

We hypothesized that slopes of the relationships between removal counts and time were due to underlying population density—that is, states with lower densities of feral swine would have negative slopes because increased removal rates were causing decreases in density so there were less feral swine being detected. Similarly, we predicted there would be positive slopes in states with high-density populations because the addition of resources for removal would lead to increased removal rates. To test this hypothesis, we regressed the estimated state-level removal rate slopes on state-level average density estimates reported in Lewis et al. (2017). We used the slope coefficients for each state from this model as the dependent variable and regressed relative feral swine density values by each state (density estimation methods described in Appendix S1).

Model of spatial spreading processes

Reduction in spatial spread of invasive species can be quantified by either observing a decrease in invasion rate (i.e., a slower rate of new invasions) or by observing a contraction in the spatial distribution. We evaluated these two components by testing for changes in invasion and extinction probabilities since the start of NFSP. We used the county-level NFSMP presence/absence (occupancy) data aggregated to the two-year time scale as described above and included an additional earlier time period (2010–2011) to allow estimation of invasion and extinction rates prior to NFSP. We modeled occupancy data using a modified dynamic occupancy model (Eq. 1-3, MacKenzie et al. 2006). A dynamic occupancy model jointly models the processes of occupancy (ψ), invasion probability (γ), and local extinction probability (ε) in county i at time t.

Occupancy analysis is a useful framework for disentangling observation error from process error when modeling species distribution data (MacKenzie et al. 2006). We assumed detection probability to be 1 because our monitoring methods were intense (i.e., see previous; multiple stakeholders, including the general public and dedicated wildlife professionals); our analysis was conducted at a coarse spatial and temporal scale (i.e., county wide within a 2-yr period, which tends to be robust to detection error; Efford and Dawson 2012); we were monitoring for establishment, rather than presence (i.e., signs of establishment are more readily detectable); and feral swine seek out and cause obvious damage to anthropogenic resources, making them easy to detect in most areas. Nevertheless, because county size is highly variable, we conducted an exploratory analysis to consider whether it affected detection probability. We hypothesized that if county size affected detection probability, there would be a positive relationship between county area and occupancy. We tested this hypothesis using a mixed logistic regression model with occupancy as the response variable; county area, invasion pressure, and time period as fixed effects; and county as a random effect (Appendix S1: Fig. S1, Table S1). The analysis showed no consistent relationship of occupancy and county area—instead the relationship of occupancy and county area depended strongly on invasion pressure and time period. Thus, we did not include county size as a predictor of detection probability and fixed detection probability at 1.

Invasion probability was modeled using logistic regression with covariate data ($X'_{i,t}$) by estimating parameters (β_γ) to explain the probability of becoming occupied given a county was not currently occupied. Local extinction probability was modeled using logistic regression with covariate data ($X'_{i,t}$) by estimating parameters (β_ε) to explain the probability of becoming unoccupied given a county was occupied. Similarly, the initial occupancy (ψ_{i1}) was modeled as a logistic regression by state funding category (a system for classifying states by annual funding allotment; described below) with parameters $\beta_{\psi.}$ This approach allowed us to estimate county-level invasion and extinction probabilities before and after the start of NFSP and examine factors that affected these invasion and extinction processes as well as initial occupancy (ψ_{i1}). Subsequent occupancy estimates ($\psi_{\mathrm{i},t}$) are derived using Eq. 4.

$$\mathrm{logit}(\psi_{i,1}) = X'_i\beta_\psi \tag{1}$$

$$\mathrm{logit}(\varepsilon_{i,t}) = X'_{i,t}\beta_\varepsilon \tag{2}$$

$$\mathrm{logit}(\gamma_{i,t}) = X'_{i,t}\beta_\gamma \tag{3}$$

$$\psi_{i,t} = (\psi_{i,t-1}(1-\varepsilon_{i,t}) + \left(1-\psi_{i,t-1}\right)\gamma_{i,t}) \tag{4}$$

For both invasion and extinction processes, we included covariate data on invasion pressure from neighboring counties (how surrounded a county is by counties with feral swine at the current time period) and management intensity (the log number of animals removed weighted by the area managed). We calculated invasion pressure as the proportion of a county's border that shared a border with occupied neighboring counties to account for effects of variable county area in neighboring counties with feral swine. To evaluate potential effects of variable county area on inference of management intensity effects, we compared models that weighted management intensity based on area managed using AIC_c (Burnham and Anderson 2002; Appendix S1: Table S2).

For invasion probability, we presented the model where current management intensity in neighboring counties was weighted by the proportion of shared border length with its neighboring counties that were experiencing control. This covariate performed similarly on invasion probability to the model without border length weighting (Appendix S1: Table S2; i.e., where management intensity on invasion probability was simply the unweighted log total number of removals in surrounding counties).

For extinction probability, which was more dependent on management within the focal county than management in the neighboring counties, we compared models where management intensity on extinction probability was weighted by the area occupied by feral swine (i.e., a density of management intensity), to models where the management intensity on extinction probability was simply the log number of removals in the focal county (Appendix S1: Table S2). For this weighting, we divided the maximum area of the county occupied by feral swine during the study (2010–2017), by the log number of removals within a county, using the NFSMS polygon data as the occupancy data. For extinction probability effects, the models without the area weighting on management intensity were more supported by the analysis (Appendix S1: Table S2) and thus were used for presentation of the results. Lastly, because management effects were cumulative over the 2-yr time scale of the analysis, it was unclear whether management intensity in the current or previous time period should be most influential on extinction probability. Thus, the choice of considering management intensity in the current versus previous time period was also made using AIC_c (Appendix S1: Table S2). For simplicity, we chose the model with the lowest absolute value of AIC_c for inference (Appendix S1: Table S3: unweighted management intensity and a one-year lag on extinction probability; weighted management intensity on invasion probability) and presentation in the results.

As there were many counties that were in regions far from invading populations, we included a dummy variable where a 1 indicated a county that had at least one occupied neighboring county during the study period, and a 0 otherwise. We reported inference for parameters related to the subset of counties with at least 1 occupied neighbor during the study period (dummy variable value = 1) because our focus was on the impact of management on spatial spread, and we were interested in spatial processes at invasion fronts, that is, invasion by natural pig movement at the edges of established populations. Although the subset of the data with the dummy variable = 0 has the potential to inform effects of translocation on invasion and extinction probabilities, we did not present these estimates because they were highly uncertain (i.e., there was not enough information in the data to estimate parameters informatively). All of the covariate data were similarly aggregated to the county level and two-year time scale to match the response data.

The NFSP determines state funding levels (0–5) based on management objectives. States with funding level 0 have the objective of preventing invasion; they included CT, DE, MD, MA, MN, MT, NE, RI, SD, and WY. States in levels 1 and 2 are aiming to eliminate early-phase invasions and prevent new invasions; they included ME, ND, WA, ID, NV, UT, CO, AZ, NE, IA, WI, MI, NY, NH, VT, NJ, OR, NM, KS, IL, IN, OH, PA, and WV. States with funding level 3 are aiming to eliminate eventually and minimize current damage; they included MO, TN, VA, KY, and MI. States with funding levels 4 and 5 have well-established populations and are aiming to minimize damage; they included CA, TX, OK, AR, LA, MS, AL, GA, SC, NC, and FL. We aggregated states with similar objectives to estimate management effects and changes in invasion probabilities. We used two separate models to estimate changes in invasion and extinction probability and test the effects of management. The objective of the management model (Appendix S1: Table S3) was to quantify the degree to which management impacted the spatial spread of feral swine. For this model, we evaluated time period, invasion pressure, and management intensity and all interactions of these covariates because we expected that management effects would depend on both proportion of the county surrounded by pigs and time period. For the management model, we estimated the effects of management on extinction probability separately for states that included an elimination objective (levels 1, 2, and 3) compared to those in levels 4 and 5 that aimed to minimize damage and level 0 that aimed to prevent invasion (Appendix S1: Table S3). We estimated effects on invasion probability separately for states with lower invasion risk (groups 0, 1, and 2) compared with states that likely have stronger invasion pressure (level 3 states that on the invasion front) and those with well-established populations (groups 4 and 5).

The objective of the second model (space-time model; Appendix S1: Table S4) was to quantify overall changes in invasion and extinction rates though space and time. This model included program classification and time period as covariates. We aggregated states with similar management objectives as with the management model. We evaluated fits of the models using an area under the curve statistic (AUC) where values above 0.7 represent a reasonable fit to the data (Fielding and Bell 1997). All statistical analyses were performed in program MARK (White and Burnham 1999).

Results

Descriptive patterns of removal effort

Since the start of the NFSP, removal of feral swine occurred in more states (Figs. 1, 2) and aerial gunning was used more often than prior to the initiation of the NFSP (Fig. 1). Prior to the NFSP, aerial gunning was mostly used in western states (e.g., TX, OK, and KS), whereas once the NFSP was initiated aerial gunning became used more widely in eastern states (Fig. 1). Similarly, more states have been able to diversify their repertoire of techniques that are used (Fig. 1). The use of ground shooting techniques has increased substantially across the nation (Fig. 1) since the start of NFSP (Appendix S1: Figs. S2, S3), while removals using snares have dropped substantially, and removals using traps have fluctuated (Appendix S1: Fig. S2, S3).

For trapping, catch per unit effort (CPUE) tended to be slightly higher during March–May and September both before NFSP and currently (Appendix S1: Fig. S4, compared thick and thin lines in the bottom right plot). For aerial gunning, CPUE during NFSP was substantially higher in December relative to other months of the year, whereas it fluctuated slightly with no clear pattern before NFSP (Appendix S1: Fig. S4). For ground shooting, CPUE patterns were similar before and after NFSP, being slightly higher in December–January and April. In general, CPUE tended to be higher after NFSP for aerial gunning and ground shooting, but the opposite was true for trapping (Appendix S1: Fig. S4).

Spatio-temporal removal trends

Overlaying the MIS database on the NFSMS database highlighted the extent of the United States with feral swine were present but no apparent control was being implemented by NFSP (Fig. 2, i.e., areas in black indicate gaps in control relative to the distribution of feral swine). Before NFSP, there were 65 ASD with feral swine reported but no control, out of 205 ASD with feral swine reported—that is, 32% of ASDs that had feral swine did not have any removal work. In 2014–2015, this first increased to 43% (78/201), but decreased to 26% by 2016–17 (46/174). Thus, overall, since the start of NFSP these areas have decreased 6%, indicating that the geographic scope of feral swine removal has increased. Similarly, as NFSP has progressed, there have been more removals in areas where feral swine had not been documented in the NFSMS data (Fig. 2). Total ASDs in contiguous United States with feral swine reported decreased from 205/329 (62%) in 2012–2013 to 174/329 (53%) in 2016–2017.

Removal rates decreased significantly over time in two states: NM and OR, but increased significantly in nine states: TX, NC, MS, SC, AL, OK, LA, MO, and KS (Appendix S1: Fig. S5). Other states with removal work (FL, CA, GA, AR VA, TN, KY, OH, WV) showed no significant

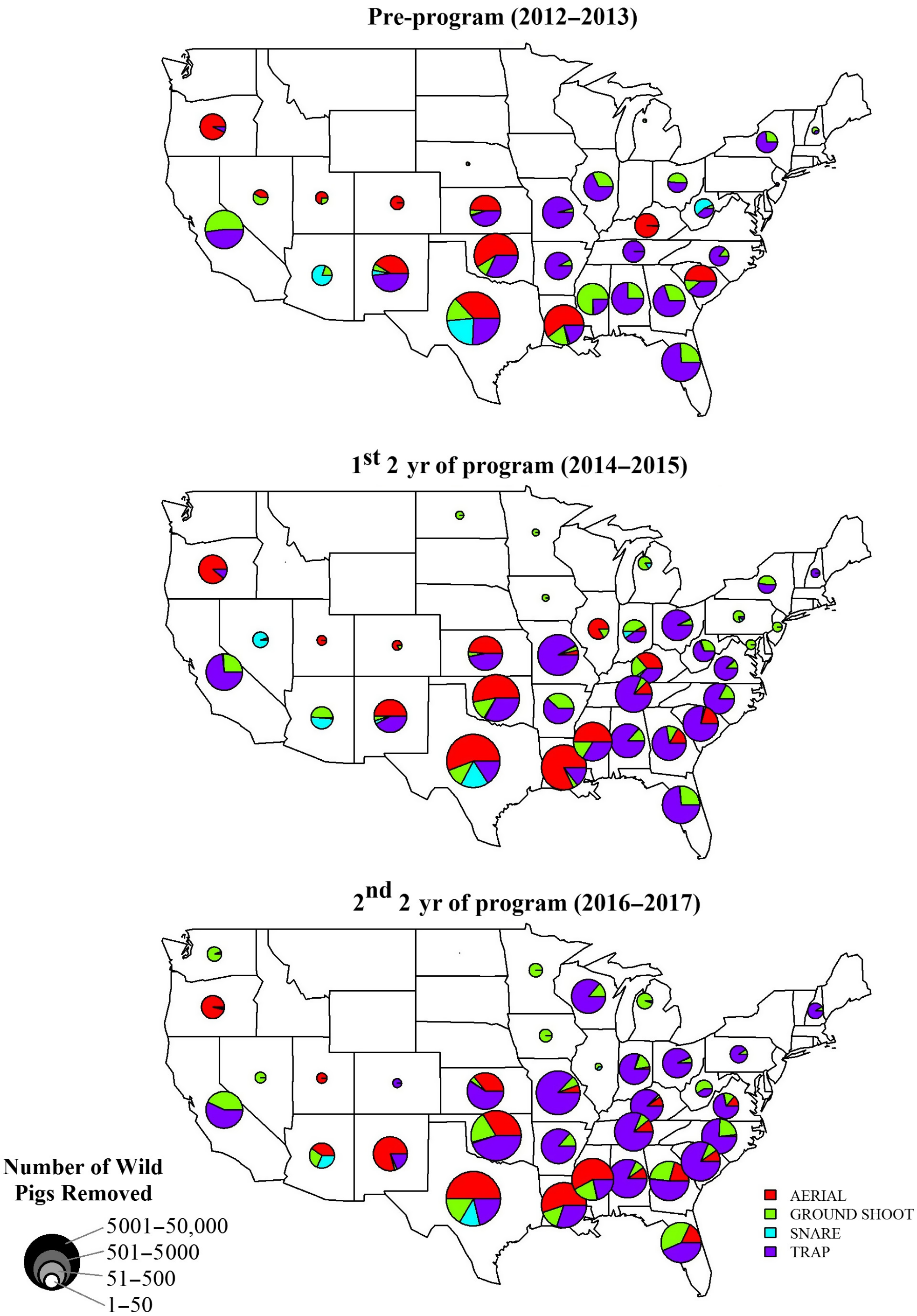

Fig. 1. Raw counts of pigs removed by each removal method. Pie charts show MIS data for each state as the proportion of removals by each method. Size of the pie chart corresponds to the total number of pigs removed in the state during the year (removal counts indicated by the gray scale circles).

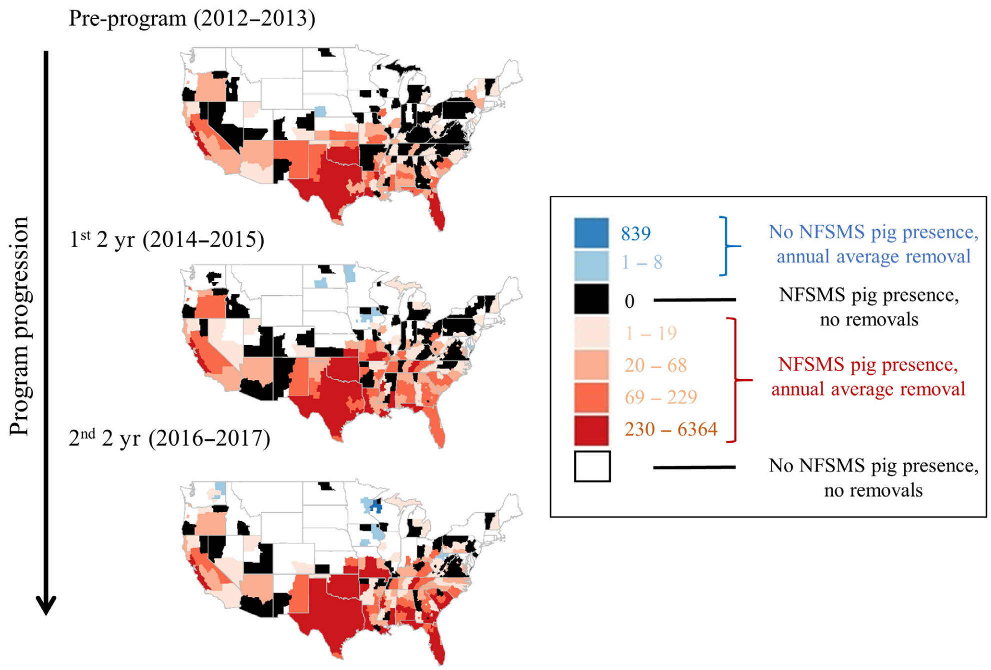

Fig. 2. Raw counts of pigs removed by ASDs and overlayed onto the pig distribution as observed in NFSMS data. Red shades show removal intensity where there are pigs. Black shows where there are pigs but no removals. Blue shades show removal intensity in areas where there is no distribution data coverage. White represents areas where pigs have not been reported.

change in removal rates (Appendix S1: Fig. S5). As hypothesized, there was a significantly positive relationship between the change in removal rates and the estimated state-level density of feral swine (Appendix S1: Fig. S6).

Effects of invasion pressure and management on spatial spread

From the raw NFSMP data (Appendix S1: Tables S5, S6), 80 more counties (from 1230 to 1310 counties) were occupied between 2010 and 2011 and 2012–2013 (prior to NFSP). Then, from 2012–2013 to 2014–2015 (during the first two years of NFSP), the total number of counties occupied was 87 more (1310–1397 counties). In contrast, by 2016–2017 there were nine fewer counties occupied relative to 2014–2015 (1397–1388 counties), indicating an increase in overall occupancy since the start of NFSP (1310–1388 counties) but a decrease in the proportion of occupied counties over time. Indeed, the occupancy model predicted that in 2012–2013, invasion probability for a county with neighboring pig populations was 0.14 (95% credible interval, CI: 0.11–0.18). This invasion probability was similar at 0.13 (95% CI: 0.10–0.17) during the first two years, but reduced significantly to 0.06 (95% CI: 0.04–0.09) during the second two years of NFSP (Fig. 3A; Appendix S1: Tables S4, S6) indicating that invasion probability had decreased by 0.08 on average. There was no significant change in extinction probability since the start of NFSP: Before extinction, probability was between 0.03 and 0.07, after it was between 0.02 and 0.05 (Fig. 3A; Appendix S1: Tables S4, S6). Thus, the overall spatial area occupied by feral swine has not been reduced yet, despite ongoing extinction in specific counties. For example, of the counties that border at least one county with a documented pig population, 62.2% were occupied in 2012–2013, and 66.4% and 65.9% were occupied in 2014–2015 and 2016–2017, respectively. Overall, results show that spatial expansion continues, but its overall rate has slowed since the start of NFSP, and elimination in specific counties has occurred.

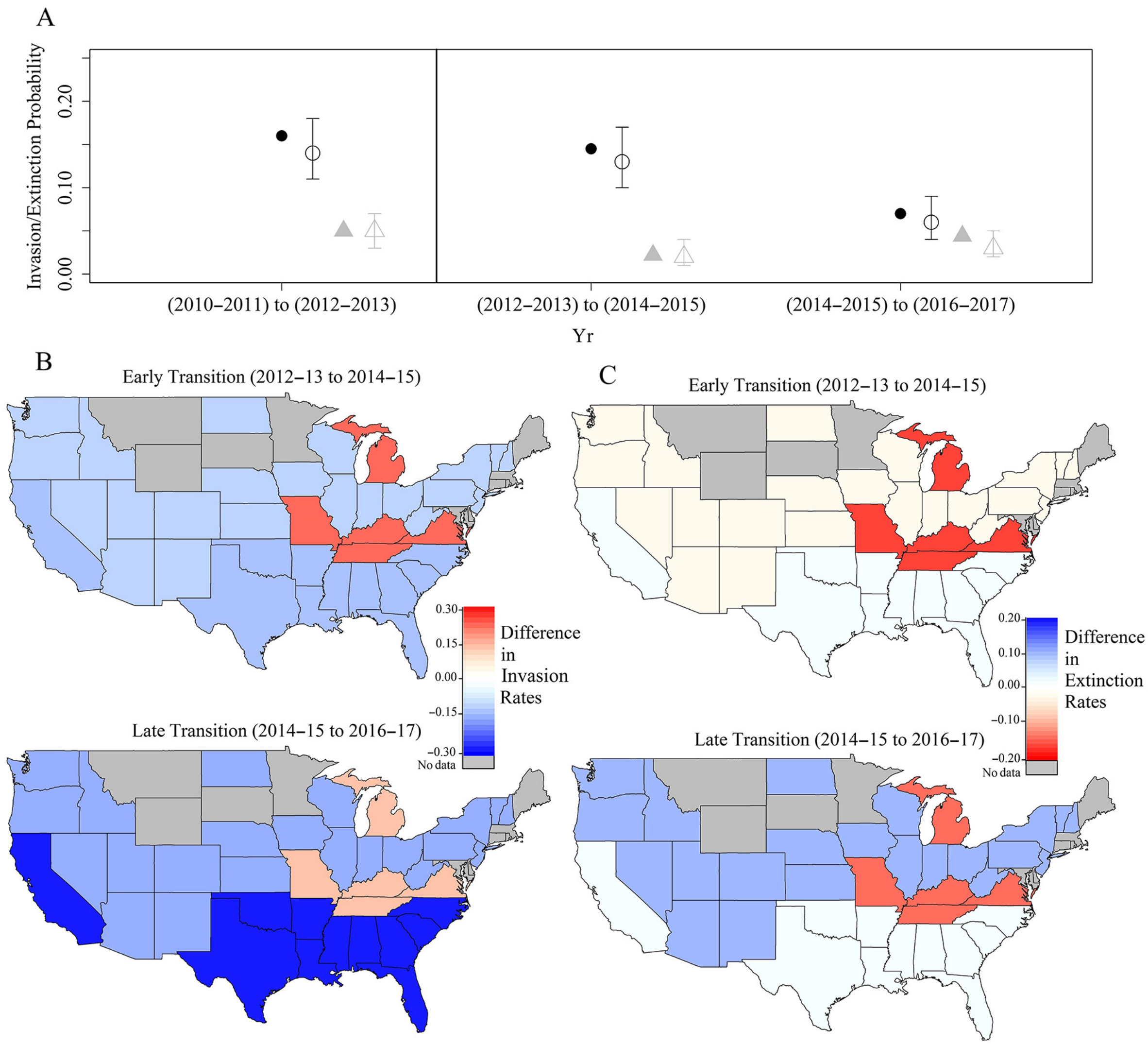

Fig. 3. Probability of invasion and extinction using space-time model. (A) Invasion (black circles) and extinction (gray triangles) probabilities for counties on average during transitions for the indicated time frames (*X*-axes). Raw data: filled symbols; model predictions: open symbols with 95% prediction intervals. (B and C) Absolute difference in the predicted proportion of counties (Appendix S1: Table S4, S6) with new invasions (B) or extinctions (C) relative to the previous time period (where 2014–2015 is compared against 2012–2013). Gray: no NFSMS data; white: no change. Red scale indicates increased invasion probability (B) or decreased extinction probability (C); blue scale indicates decreased invasion probability (B) or decreased extinction probability (C).

For example, in 2012–2013 the estimated invasion probability was between 0.11 and 0.18, which predicts that between 89 and 145 counties (out of 807 available) were newly invaded. If this invasion rate in available counties continued, there would have been between 86 and 141 new counties (out of 782 available) and between 89 and 146 new counties (out of 810 available) invaded in 2014–2015 and 2016–2017, respectively, for a total of between 175 and 287 counties newly invaded (231 on average). However, based on the changes in invasion probability over time that we estimated from the occupancy model, we predicted that only between 78 and 133 counties (out of 782) were invaded in 2014–2015 and between 32 and 73 (out of 810) were newly invaded in 2016–2017 for a total of between 110 and 206 newly invaded counties (158 on average), a difference of 73 counties on average. Applying the same logic but restricting the predictions to only counties in the level 0–2 funding categories, the model predicted that between 122 and 178 counties would have been newly invaded since the start of NFSP if invasion rates were maintained at pre-program levels, but instead only between 13 and 41 counties were newly invaded (i.e., demonstrating a significant reduction in the number of newly invaded counties), a difference of 122 counties on average.

Although invasion probability has decreased, the strength of the effect varied significantly by time period and funding level (Fig. 3B; Appendix S1: Tables S4, S6). Relative to before NFSP, invasion probability after 4 yrs of NFSP decreased significantly by 0.15 on average in states with funding levels 0–2 and by 0.27 on average in states with funding levels 4–5 (Appendix S1: Table S6). In states with level 3 funding, invasion probability first increased significantly by 0.19 and then decreased substantially by 0.08 for a net increase of 0.11 on average since the start of NFSP (Appendix S1: Table S6).

Invasion probability increased and extinction probability decreased significantly with invasion pressure (IP in Appendix S1: Table S3; Fig. 4). As expected, there was a significant interaction between invasion pressure and management intensity for invasion probability (extinction probability showed a non-significant trend), thus we showed model predictions for low (10% of neighbors with pigs) versus high (50% of neighbors with pigs) invasion pressure. At low invasion pressure, there was a trend of decreased invasion probability and increased extinction probability (although only for the later time period) with increased management intensity (Fig. 4, middle; Appendix S1: Table S3), but there were no such trends under high invasion pressure (Fig. 4, right; Appendix S1: Table S3).

Discussion

Expansion rates of established invasive species can vary spatially due to landscape and anthropogenic factors (McClure et al. 2015, Tabak et al. 2017). By considering local variation in invasion rates (invasion pressure), we demonstrated a decrease in the rate of spatial spread of an invasive species at the national scale since the start of enhanced control. Additionally, the concept of separating spatial spread processes into invasion and extinction is important to consider because changes in invasion rates may not be obvious but could demonstrate substantial management effects, for example, new invasions may continue to occur but their rate is reduced. Based on predictions of decreased invasion rate from the occupancy model, we predicted that invasion was prevented in 73 counties on average (9.2% of counties available in 2012–2013) by 2016–2017, with a minimum of 0 and a maximum of 177. While uncertainty is fairly large in these estimates that consider all states, if we consider only counties in the level 0–2 funding category, the predicted number of counties where invasion is prevented is between 81 and 165, or 122 on average (27.7% of available counties in 2012–2013), a highly significant number.

A caveat is that because we did not have independent controls, we could not distinguish whether the decreased proportion of counties with new invasions was due to management alone or whether some other processes contributed. Indeed Snow et al. (2017*a*) found that the rate of spatial invasion increased dramatically from 1982 to 2009 but was slightly lower in 2009–2012 relative to 2004–2009 suggesting some slowing of spread. We rationalize, though, that this decreased rate of spread could also have been due to increased management because during 2009–2012 increased policies and efforts for controlling feral swine were already being implemented (Miller et al. 2018).

Going forward, it would be valuable to establish long-term monitoring sites using a case and control design. Sites could have similar invasion pressure and differing management (including no management), to quantify factors that are causing the observed decrease in invasion rates. Additionally, while we assumed detection probability was 1 (see *Methods*), there is likely some low level of misclassification that occurred. A dedicated monitoring program would serve to collect data that could inform detection probability to reduce potential bias in estimates of occupancy processes and provide

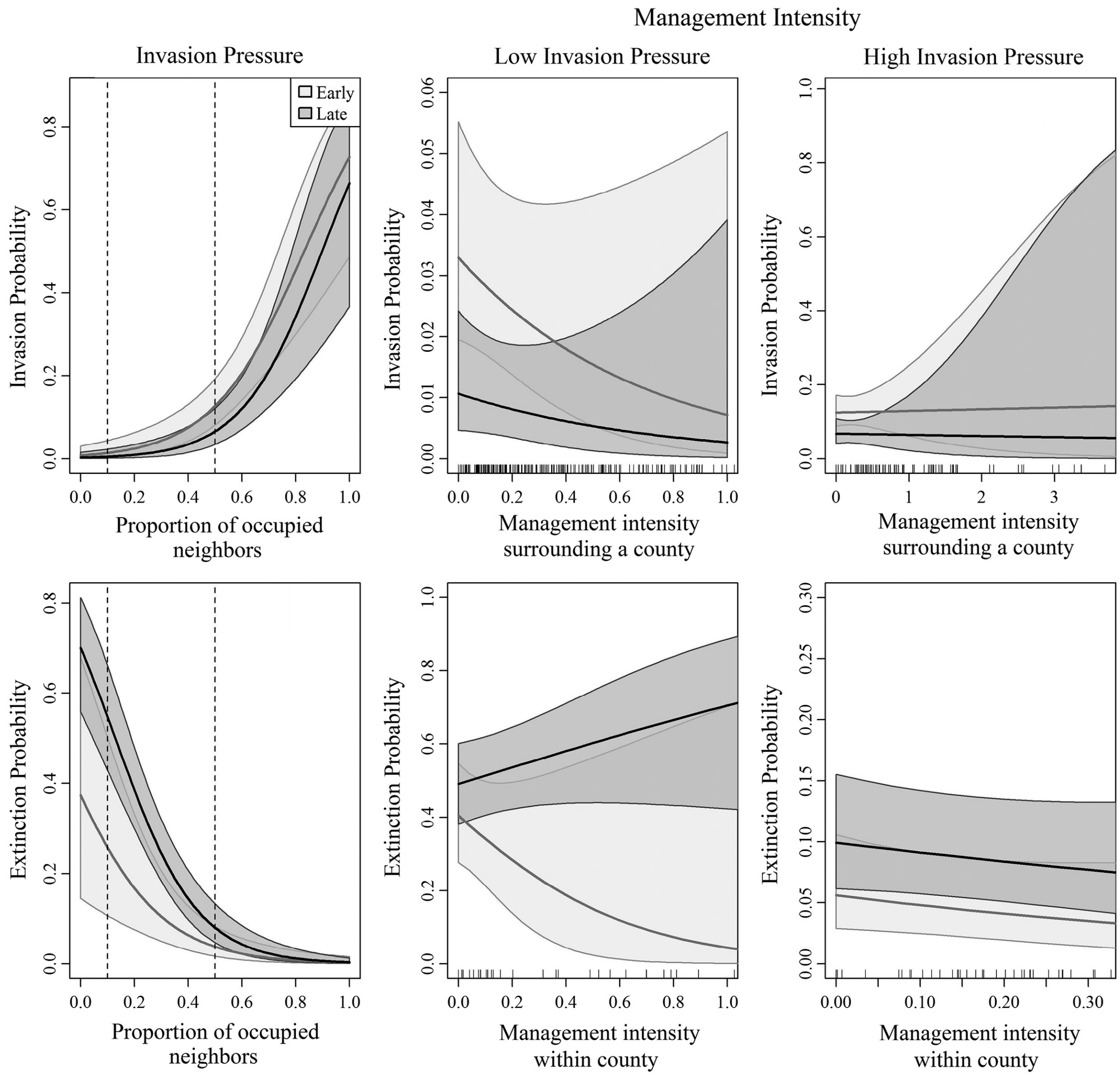

Fig. 4. Effects of invasion pressure and management for 2014–2015 (early) and 2016–2017 (late). Predictions of invasion (top) and extinction probabilities (bottom) from the management model (Appendix S1: Table S3) with 95% prediction intervals (shading). Left plots show the relationship of invasion and extinction probabilities as a function of invasion pressure. The vertical lines show the values of invasion pressure that are used in the middle and right plots. Middle and right plots show the effects of management intensity on invasion and extinction probabilities.

guidance for improved surveillance in low-density regions.

Estimates of reduction in spatial invasion rates provide the foundation for estimating economic benefits in terms of the cost of damage prevented by management programs, that is, quantifying the effort–outcomes relationship (Hone et al. 2017). To illustrate this concept, consider that the average damage to six crops (corn, soybeans, wheat, rice, peanuts, and sorghum) in 2014 in North Carolina (a state with unoccupied counties adjacent to occupied counties) was US$4,684,000

(Anderson et al. 2016), or US$64,164 per county on average among the 73 counties with feral swine in 2014 (Appendix S1: Table S5). Our results suggest that if invasion were prevented in 122 counties with similar damage potential, this may have prevented US$7,828,008 in damage to the six crops alone. Of course, this is an oversimplification because damage estimates depend on the specific commodities and natural resources that are present in counties available for invasion (which varies widely nationally), and the estimates are only for six crops—excluding damage to other crops, natural resources, and livestock. The value of losses also depends on the density of feral swine, not presence alone. That is, damages would start out smaller before reaching these high levels that were calculated in areas where there are well-established populations. Nonetheless, in the longer term, prevention of invasion could have large financial savings that are an important component of valuation of overall economic savings attributed to NFSP. Our approach provides a component of this valuation process—estimates of where invasion has been prevented—that can be combined with location-specific commodity and damage rate data for valuation of the damage prevented. Similar logic could be applied to estimate the value of damage prevented in terms of other resources such as natural resources, recreation opportunities, personal or commercial property, or livestock disease risk. Additionally, our results can inform the overall cost-benefit value of NFSP itself, by adding the monetary benefits from decreased rates of spatial spread with the monetary benefits of reducing damage in high-density areas (not quantified here), weighed against the costs of program implementation.

Our descriptive summaries showed that NFSP has (1) led to increased use across the country of the most effective removal techniques for feral swine, (2) increased removal overall, and (3) facilitated removal in areas where it was not previously occurring. Illustrating these changes is important for justification of how NFSP funding allocations are being applied. While these trends in implementation of removal techniques do not themselves reveal impacts of an invasive species control program, they provide guidance for prioritization of resources and the design of research studies that could evaluate the impact of these changes on damage. Especially for large-scale programs, understanding how resources are being used across space and time can be obscure, but is important for evaluating cost-effectiveness of different local management strategies.

We observed substantial shifts in usage of different methods of removal across the country, for example there has been increased use of aerial gunning and ground shooting techniques since the start of NFSP. It is well known that the efficacy of different methods of removal varies by habitat and population density (Choquenot et al. 1999, West et al. 2009). Thus, in addition to increasing overall removals, these changes could be increasing the efficacy of removal by expanding the repertoire of methods available in different areas. Research to quantify the cost-effectiveness of different methods of removal in different ecoregions and population densities is needed to understand whether the allocation of resources by NFSP funding is optimal. Such research studies would also provide essential data for developing science-based approaches for optimizing management strategies adaptively in space and time. Also, some research funding from NFSP is going toward the development of new methods such as toxicants (e.g., Snow et al. 2017*b*) and fertility control (see Pepin et al. 2017*a, b* for theoretical evaluation). These are investments that have not yet been realized in terms of feral swine removals. Another potential indirect effect is that the NFSP has brought personnel, expertise, and equipment infrastructure to states that previously had limited infrastructure. When cooperative stakeholders share costs, overall impact could be higher than would have been possible without the cooperation (e.g., state management programs that use NFSP infrastructure for cost-sharing). These effects of national-scale programs are more difficult to quantify, but are important to consider in overall assessment.

There were clear patterns of efficiency that are important to consider in national-scale resource allocation planning. For example, CPUE for aerial gunning was dramatically higher in the early fall and month of December, yet effort has been highest in March and April—indicating a potential inefficiency. In contrast, CPUE has clear peaks in December–April for ground shooting and March–May and September for trapping, yet effort by ground shooting tended to be lowest in December–January and effort for trapping tended to be fairly consistent with slight increases in July–October. Thus, it seems that emphasizing aerial gunning in the fall and December, and emphasizing other techniques in the spring (and trapping in the fall as well) could be most efficient. In addition, previous work has shown that prioritizing removals during non-birthing periods can improve the efficiency of control (Pepin et al. 2017*a,b*), suggesting that further optimization of timing could be helpful. However, our results are national-scale averages and previous work has indicated that forage availability can greatly impact feral swine population growth and establishment (Tabak et al. 2018). Thus it is possible that these trends could vary by state due to differences in feral swine birth dynamics, resource availability, the amount of removal that is occurring by non-NFSP mechanisms (e.g., state/county/other Federal partners and private landowners), and state-level management plans. A state-level CPUE analysis could help to identify potential inefficiencies at a more appropriate spatial scale, which could then be used to guide research to identify optimal strategies for application of different removal techniques. Also, management plans can not only depend on optimal resource allocation in terms of the spatio-temporal efficacy of different management techniques, but must also consider requests by landowners to mitigate current conflicts. Thus, frequency of access to private lands is dependent on when cooperators allow/request work to be done. Adaptive management tools that include both landowner availability and efficacy of different techniques in space and time could help to optimize program performance.

An unexpected trend in our analyses was that CPUE for trapping tended to be higher before NFSP relative to after NFSP. A potential explanation for this is that the NFSP, which has an explicit goal of feral swine elimination, has increased trapping areas where feral swine are rare. As CPUE decreases with population densities (McCann and Garcelon 2008), trapping in more areas where feral swine are rare could lead to an overall decrease in CPUE. A second reason for a decrease in CPUE from trapping could be that, since the start of the NFSP, there has been a large influx of less experienced trappers, and trapping work has expanded into new habitats where trapping techniques, including baits and lures, have not yet been optimized. For example, the attractiveness of specific baits can be relative to other local resources (Lavelle et al. 2017). Trapping efficiency could likely be improved in areas where feral swine are rare or where baits are less effective by investing research in new baits and lures that are intensely attractive over a variety of ecological conditions (Lavelle et al. 2017).

We also found that state-level removal rates have both increased and decreased since the start of the NFSP and that the state-level variation in removal rates can be partly explained by feral swine densities prior to the start of the NFSP. This is consistent with our hypothesis that in high-density states, removal rates might increase as more resources are invested into removing feral swine because densities are high enough that removals are not affecting them (thus adding more resources allows for removal of more feral swine). In contrast, we expected that increased resources in low-density states should lead to lower removal rates over time as the increased resources could impact the density, making it more difficult to remove feral swine in the future. Although our results were consistent with this density hypothesis, underlying feral swine densities are not the only possible explanation for state-level variation in removal rates. Feral swine populations could learn to avoid some control methods, which could be another factor leading to decreased removal rates over time (Choquenot et al. 1996).

Extinction probabilities did not increase significantly, and there was an overall increase in occupied counties. Thus, nationally the area occupied by feral swine has not contracted significantly, despite elimination ultimately being an objective in several areas. One likely reason is that measurable impacts can be delayed even when management is being effective. Indeed, in all areas, invasion rates decreased even more during the second two years relative to the first two years of NFSP indicating that progress is occurring. Even in level 3 states where invasion rates increased relative to pre-program levels, we found that invasion rates decreased during the second two years of NFSP relative to the first two years. One reason for the lagged effects (or a lack of detecting effects) is that we were focused on occupancy (presence/absence status)—the threshold of a county changing from 1 to 0. Counties with more pigs will be delayed in making that transition because substantial effort and time are required to locate and remove individuals when the population is abundant. An analysis of the effects of management intensity on decreasing densities would be valuable for understanding the cause of lagged effects.

For interpreting the meaning of changes in invasion rates, it is critical to consider both the invasion potential and the management objective in different areas. In level 3 states, the objective is to locate undetected feral swine populations and reduce damage caused by their presence. Feral swine populations are typically well established (moderate population densities) in several isolated, distinct areas (Hartin 2006). Invasion rates in level 3 states were only slightly decreased during the second two years relative to the first two years and remained higher than pre-program levels during both time periods of NFSP. This increased rate of invasion is likely because invasion potential is high in these states (e.g., MO, TN, VA, and KY) because there are many unoccupied counties in these states (68.2% in 2012–2013 to 43.9% in 2016–2017 on average) that surrounded dense, productive populations. Well-established populations in these areas can continue to produce many offspring for dispersal to new areas posing a continued high risk of new populations being established. Because one of the NFSP objectives is to locate feral swine populations, increased detection may be contributing to apparently increased invasion rates relative to pre-program levels (when fewer populations were detected).

In level 0–2 states, the objectives are early detection removal, invasion prevention, and elimination. In these states, feral swine populations occur at very low densities but have potential to invade new areas (McClure et al. 2015, Snow et al. 2017*a*). Thus, decreased invasion rates may indicate a substantial reduction in invasion risk. Even in level 2 states, where feral swine populations are established at low densities, and the primary objective is to work toward elimination, and invasion rates decreased from pre-program levels during both time periods (2014–2015 and 2016–2017), despite the high availability of unoccupied counties. In contrast, in level 4–5 states, the management objectives are to reduce feral swine populations and minimize the damage caused by them, thus elimination is not an objective. Feral swine populations are well established across these states and few counties are unoccupied (ranging from an average of 6% in 2012–2013 to 4% in 2016–2017, with some states being below 1% by 2016–2017; Appendix S1: Table S6). Thus in these states, reductions in the proportion of counties with new invasions could be partly due to the recent low levels of invasion potential. A more informative metric of program performance in these states is the proportional reduction in density and its relationship to value of damage reduction —an important goal for future work.

One of the biggest challenges with management of feral swine is translocation of pigs by humans, sometimes over long distances. Translocation has been documented in several countries (Spencer and Hampton 2005, Goedbloed et al. 2013, Tabak et al. 2017, Hernandez et al. 2018). In the United States, translocation is a common practice (Tabak et al. 2017, Hernandez et al. 2018) despite some states having regulations against the importation and release of feral swine (Centner and Shuman 2015). In cases where new populations are established from long-distance sources, management in neighboring counties may have little impact. In fact, one of the challenges that managers face is the propensity for the public to re-establish pigs once management has driven their populations to low levels. Thus, a naïve analysis of management effects on the proportion of counties with new invasions could appear to show no effects on or increased invasion potential in heavily managed areas with high rates of anthropogenic introduction. While intentional anthropogenic movement may not be as pervasive for invasive pests that have low value by the general public, it is a major issue for a species such as feral swine which can have high value to many members of the public (e.g., in terms of hunting opportunities, food, or landowner revenue; Adams et al. 2005, Weeks and Packard 2009). Nonetheless, even for invasive species of low value, unintentional long-distance movement can lead to similarly complex spatial expansion patterns (Garnas et al. 2016). One way to account for the non-local spread is to conduct genetic analyses. Tracking genotypes for a portion of individuals removed during a management program could provide valuable spatial connectivity data for quantifying management effects.

Another application of invasion analysis could be for spatial prioritization of resources. Although we only presented average results grouped to the funding level classifications, it would be straightforward to identify states or groups of counties within those classifications that have higher than average invasion probabilities. Accounting for regional predictions of the proportion of counties with new invasions with potential damage that could be caused by feral swine in those regions would highlight where the risk of new losses and invasion are concurrently highest. Incorporating estimates of the proportion of areas with new invasions into risk assessment methodology is useful for prioritizing resource allocation (Gallardo and Aldridge 2013, Booy et al. 2017) and providing decision-support tools such as systematic conservation planning (McIntosh et al. 2017).

Conclusions

Prioritizing resources to areas where feral swine are known to be present but where there is currently little or no management (light peach and black areas in Fig. 2) and where rates of new invasions are highest (as predicted by the spread model) could help to accelerate overall damage reduction by maximizing the damage prevented. This prioritization will involve both increased management intensity on lands for which there is an active agreement and engaging more landowners. Similarly, state-level evaluation of CPUE by different removal techniques combined with landowner availability data could be linked in a decision-support tool to help optimize which techniques should be prioritized seasonally. Although our analyses do not demonstrate differences in cost-effectiveness of different removal techniques in space and time, the trends we showed emphasize that research to understand how cost-effectiveness of different suites of techniques varies across space and time could be important for informing the decision-support tool. More broadly, our analysis provides a conceptual foundation for evaluating large-scale programs and emphasizes the importance of developing evaluation frameworks before program implementation to help guide prioritization of resources and maintain funding from stakeholders. The next important step will be to combine estimates of decreased invasion with distributions of commodities, natural resources, or sensitive species and their associated values in order to estimate the value of damage prevented. Once the value of damage prevented is estimated, it can be balanced against invasion risk estimates (as we present here) to determine spatial management plans that would maximize the damage prevented.

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Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2657/full

Ecosphere

Appendix S1

Accounting for Heterogeneous Invasion Rates Reveals Management Impacts on the Spatial Expansion of an Invasive Species

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METHODS

State-level density estimates

State-level estimates of feral swine density were predicted from the fitted model developed in Lewis et al. 2017. Briefly, this approach involved multiple linear regression of wild pig density estimates around the globe as the dependent variable, and biotic and abiotic data as the independent variables. Predictions were made at 1 km^2 resolution. We used this model to predict feral swine densities within the polygons of feral swine occurrence in 2013 as determined by the NFSMS for the 20 states that we estimated removal rates (AL, AR, CA, FL, GA, KS, KY, LA, MS, MO, NM, NC, OH, OK, OR, SC, TN, TX, VA, WV). We took the average of the 1 km^2-resolution predictions within the polygons of occurrence within each state to be the average state-level feral swine densities. We then rescaled these absolute densities by dividing each by the maximum state-level absolute density to transform the absolute state-level densities into relative densities.

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Supplementary Tables

Table S1. Generalized linear mixed-effects model fit for occupancy with county area, invasion pressure, and time period as fixed effects, and county as a random effect. This analysis was to examine the effects of variable county area on reporting occupancy. If county area is an important contributor to detecting occupancy we would expect a significant positive relationship between occupancy probability and county area. The results show that invasion pressure has the most significant effect on predicting occupancy probability.

Model information:

Number of observations	1956
Fixed effects coefficient	8
Random effects coefficient	978
Covariance parameters	3
Distribution	Binomial
Link	Logit
FitMethod	MPL

Formula:

Y ~ 1 + time*pressure + time*area + pressure*area + time:pressure:area + (1 + time | county)

Model fit statistics:

AIC	BIC	LogLikelihood	Deviance
9693.3	9754.7	-4835.6	9671.3

Fixed effects coefficients (95% CIs):

Name	Estimate	SE	tStat	DF	pValue	Lower	Upper
(Intercept)	-1.59	0.31	-5.20	1948	2.2E-07	-2.19	-0.99
time	-0.29	0.12	-2.31	1948	0.02	-0.53	-0.04
pressure	1.09	0.69	1.58	1948	0.11	-0.26	2.44
area	**-8.1E-05**	**6.4E-05**	**-1.26**	**1948**	**0.21**	**-2.1E-04**	**4.5E-05**
time:pressure	1.86	0.28	6.65	1948	3.9E-11	1.31	2.41
time:area	8.2E-05	2.8E-05	2.89	1948	0.004	2.6E-05	1.4E-04
pressure:area	4.9E-04	2.1E-04	2.37	1948	0.018	8.4E-05	9.0E-04
time:pressure:area	-2.1E-04	7.4E-05	-2.87	1948	0.004	-3.6E-04	-6.8E-05

Random effects covariance parameters:
Group: county (489 Levels)

Effect1	Effect2	Type	Estimate
(Intercept)	**(Intercept)**	**std**	1.423
time	**(Intercept)**	**corr**	-0.5546
time	**time**	**std**	0.43867

Table S2. Model selection results for covariate data in the Management Model. We considered models with and without weighting for county area differences on management intensity. For invasion probability, weighting meant that the log total number of removals in surrounding counties was weighted by the border length of the counties that had removals. For extinction probability, weighting meant that the log total number of removals in the focal county were divided by the maximum area occupied by pigs during 2010-2017 (similar to a management intensity 'density'). We also considered whether management intensity (MI) acted more strongly on extinction probability in the current time period or at a one year lag. L: likelihood; k: number of parameters.

Model differences	**AICc**	**Delta AICc**	**AICc Weights**	**Model L**	**k**	**Deviance**
Extinction: Unweighted MI; Lag on MI. Invasion: Weighted MI	3907.6	0.00	0.61	1.00	37	3833.3
Extinction: Unweighted MI; Lag on MI. Invasion: Unweighted MI	3908.5	0.89	0.39	0.64	37	3834.2
Extinction: Unweighted MI; No lag on MI. Invasion: Weighted MI	3919.4	11.9	0.00	0.00	38	3843.2
Extinction: Unweighted MI; No lag on MI. Invasion: Unweighted MI	3920.3	12.8	0.00	0.00	38	3844.1
Extinction: Weighted MI; Lag on MI. Invasion: Weighted MI	3923.3	15.7	0.00	0.00	36	3851.1
Extinction: Weighted MI; Lag on MI. Invasion: Unweighted MI	3923.5	15.9	0.00	0.00	37	3849.3
Extinction: Weighted MI; No lag on MI. Invasion: Weighted MI	3924.6	17.1	0.00	0.00	38	3848.4
Extinction: Weighted MI; No lag on MI. Invasion: Unweighted MI	3926.2	18.6	0.00	0.00	37	3852.0
Extinction: No MI. Invasion: No MI.	3943.8	36.2	0.00	0.00	23	3897.7

Table S3. Parameter estimates and goodness of fit for the top Management model (highlighted in Table 2).

Index	Label	Estimate	SE	LCI	UCI
Ψ	**Intercept**	2.3	0.17	2.02	2.67
	Level 0 (initial Ψ)	-6.1	0.38	-6.79	-5.32
	Level 1 (initial Ψ)	-5.4	0.27	-5.96	-4.91
	Level 2 (initial Ψ)	-3.8	0.20	-4.22	-3.44
	Level 3 (initial Ψ)	-3.2	0.19	-3.60	-2.85
	Level 4 (initial Ψ)	-0.3	0.21	-0.69	0.13
ε (local area not occupied)	**Intercept**	29.1	0.90	27.3	30.9
ε (local area occupied)	**Intercept**	-6.88	0.58	-8.01	-5.75
	Level 0	1305.9	2.55	1300.91	1310.90
	Level 123	7.39	0.64	6.13	8.64
	2010-11 to 2012-2013 (T1) in Level 123	0.45	0.42	-0.37	1.27
	2012-13 to 2014-2015 (T2) in Level 123	-0.28	0.46	-1.20	0.63
	Invasion pressure (IP) in Level 123	-5.42	0.77	-6.94	-3.91
	Within-county management in *t*-1 (WM) in Level 123	1.36	0.85	-0.30	3.03
	IP x WM in Level 123	-4.57	2.85	-10.15	1.02
	T1 x IP in Level 123	-1.49	1.27	-3.98	1.00
	T1 x WM in Level 123	14.92	928.03	-1804.01	1833.86
	T1 x IP x WM in Level 123	27399	0.20	-27399.76	-27398.99
	T2 x IP in Level 123	-0.66	1.35	-3.30	1.99
	T2 x WM in Level 123	-4.32	2.51	-9.24	0.61
	T2 x IP x WM in Level 123	7.16	4.98	-2.60	16.91
γ (local area not occupied)	**Intercept**	-4877	0.00	-4877	-4877
	Level 012	-2266	1.47	-2269	-2263
γ (local area occupied)	**Intercept**	-5.01	0.80	-6.58	-3.44
	T1	1.92	0.53	0.89	2.95
	T2	1.27	0.56	0.17	2.37
	IP	4.42	1.08	2.29	6.54
	Neighbor management in *t* (NM)	-3.89	2.27	-8.33	0.56
	IP x NM	7.19	3.25	0.82	13.56
	T1 x IP	-1.59	0.87	-3.29	0.11

T1 x NM	2.05	1.73	-1.34	5.43
T1 x IP x NM	-3.01	2.63	-8.16	2.14
T2 x IP	-1.20	0.89	-2.95	0.55
T2 x NM	-0.23	1.78	-3.73	3.26
T2 x IP x NM	0.65	2.71	-4.67	5.97
Level 012	0.00	0.70	-1.36	1.37
Level 3	-0.99	0.74	-2.45	0.47
IP x Level 012	0.35	0.97	-1.55	2.25
IP x Level 3	3.06	1.03	1.05	5.08
NM x Level 012	2.17	1.77	-1.31	5.65
NM x Level 3	3.43	1.96	-0.41	7.27
IP x NM x Level 012	-3.86	2.40	-8.58	0.85
IP x NM x Level 3	-6.06	2.78	-11.50	-0.62

AICc = 3907.6
AUC with all data = 0.80
AUC with subset data = 0.78 (only data that had at least one transition)

Table S4. Parameter estimates and goodness of fit for the Space-Time model.

Index	Label	Estimate	SE	LCI	UCI
Ψ	**Intercept**	2.3	0.17	2.02	2.67
	Level 0	-6.1	0.38	-6.79	-5.32
	Level 1	-5.4	0.27	-5.96	-4.91
	Level 2	-3.8	0.20	-4.22	-3.44
	Level 3	-3.2	0.19	-3.60	-2.84
	Level 4	-0.3	0.21	-0.69	0.13
ε (local area not occupied)	**Intercept**	-0.1	0.00	-0.13	-0.13
ε (local area occupied)	**Intercept**	-6.9	0.58	-8.02	-5.75
	Level 0	18.9	0.00	18.85	18.85
	Level 0 x T1	18.9	0.00	18.85	18.85
	Level 0 x T2	-0.1	0.00	-0.10	-0.10
	Level 12	5.9	0.60	4.72	7.08
	Level 12 x T1	-0.6	0.29	-1.12	0.00
	Level 12 x T2	-0.8	0.27	-1.29	-0.24
	Level 3	3.7	0.67	2.44	5.06
	Level 3 x T1	1.7	0.40	0.93	2.50
	Level 3 x T2	-1.8	1.06	-3.88	0.28
γ (local area not occupied)	**Intercept**	-17.9	460.1	-919.8	884.0
	Level 012	-4.2	306.6	-605.2	596.7
γ (local area occupied)	**Level 012**	-5.0	0.58	-6.13	-3.86
	Level 012 x T1	3.3	0.59	2.14	4.46
	Level 012 x T2	2.0	0.62	0.78	3.22
	Level 3	-1.5	0.17	-1.87	-1.18
	Level 3 x T1	-1.1	0.29	-1.65	-0.51
	Level 3 x T2	0.5	0.22	0.03	0.89
	Level 45	-1.7	0.41	-2.47	-0.86
	Level 45 x T1	1.4	0.46	0.49	2.28
	Level45 x T2	0.8	0.50	-0.18	1.77

AICc = 4514.5
AUC with all data = 0.94
AUC with subset data = 0.88 (only data that had at least one transition)

Table S5. Descriptive summary of state-level changes.

		Level	Number of counties occupied											
State	**Counties**	**2014**	**2004**	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**Status**
Connecticut	**8**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Delaware	**3**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Maryland	**24**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Massachusetts	**14**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Minnesota	**87**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Montana	**56**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Nebraska	**93**	**0**	2	9	9	9	9	0	0	0	0	0	0	
Rhode Island	**5**	**0**	0	0	0	0	0	0	0	0	0	0	0	
South Dakota	**66**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Wyoming	**23**	**0**	0	0	0	0	0	0	0	0	0	0	0	
Maine	**16**	**1**	0	0	0	0	0	0	0	0	0	0	0	
New York	**62**	**1**	0	3	3	4	4	10	10	**10**	**0**	**0**	**0**	Extinction
Iowa	**98**	**1**	1	1	1	1	1	2	2	**1**	**1**	**1**	**0**	Extinction
New Jersey	**21**	**1**	0	0	3	3	2	2	2	**2**	**1**	**1**	**0**	Extinction
Colorado	**64**	**1**	1	3	3	3	3	3	3	3	1	1	1	
Idaho	**44**	**1**	0	0	0	1	1	1	1	1	1	1	1	
North Dakota	**53**	**1**	0	1	1	1	1	1	1	1	1	1	1	
Washington	**37**	**1**	0	1	1	1	1	0	0	0	1	1	1	
Wisconsin	**72**	**1**	0	1	1	1	1	3	3	3	1	1	1	
New Hampshire	**10**	**1**	1	1	2	2	2	3	3	3	3	3	2	
Nevada	**17**	**1**	3	3	3	3	3	3	3	3	2	2	3	
Utah	**29**	**1**	0	0	0	0	0	3	3	3	3	3	3	
Vermont	**14**	**1**	0	0	0	0	0	4	4	4	3	3	3	
Arizona	**15**	**1**	4	4	4	4	4	8	8	8	6	6	3	
Illinois	**102**	**2**	0	0	4	7	7	8	8	1	5	5	2	
Indiana	**92**	**2**	11	11	11	10	10	22	22	7	4	4	3	
Pennsylvania	**67**	**2**	0	2	2	2	2	19	19	23	13	13	4	
Oregon	**36**	**2**	8	18	18	18	18	18	18	18	18	18	8	
Kansas	**105**	**2**	16	16	22	22	22	21	14	12	9	9	9	
West Virginia	**55**	**2**	0	0	0	0	0	8	8	8	12	12	12	
New Mexico	**33**	**2**	12	12	12	11	11	19	19	19	15	15	12	
Ohio	**88**	**2**	7	22	32	34	24	23	24	18	23	23	18	
Michigan	**83**	**3**	0	0	1	47	18	19	19	17	18	18	1	
Virginia	**95**	**3**	3	3	7	10	10	20	20	20	22	22	25	
Missouri	**115**	**3**	23	38	38	38	38	38	38	38	42	45	44	
Kentucky	**120**	**3**	11	12	13	14	14	17	17	5	64	64	56	
Tennessee	**95**	**3**	36	40	40	40	40	46	46	46	57	57	77	
South Carolina	**46**	**4**	43	43	43	43	43	45	45	41	46	46	46	
louisiana	**64**	**4**	61	61	61	61	62	62	62	60	62	62	62	
Alabama	**67**	**4**	63	63	63	63	63	64	64	64	67	67	67	
Arkansas	**75**	**4**	59	69	68	70	70	72	72	71	73	73	73	
North Carolina	**100**	**4**	59	60	63	65	68	71	71	73	76	76	82	
Mississippi	**82**	**4**	79	79	79	79	79	81	81	78	81	82	82	
Georgia	**159**	**4**	140	139	139	141	141	142	142	141	146	146	146	
California	**58**	**5**	57	57	57	57	57	57	57	54	57	57	57	
Florida	**67**	**5**	66	65	65	65	65	65	65	64	66	66	66	
Oklahoma	**77**	**5**	51	52	56	56	56	76	76	74	75	75	76	
Texas	**254**	**5**	238	238	238	238	238	253	253	253	253	253	253	

Table S6. Summary of spatial spreading processes estimated from the Space-Time Model (also summarized in Figure 5 of the main text). Only estimates for counties with at least one occupied neighbor are reported (i.e., dummy variable = 1). The 'All' rows are derived from weighted averages of invasion and extinction probabilities from estimates within each funding level using the unoccupied and occupied counties as weights, respectively.

Level in 2014	States	Objectives	Period	Counties Occupied	Counties Unoccupied	Proportion Occupied	Counties with at least one occupied neighbor: Invasion Probability			Extinction probability		
							Mean	Lower	Upper	Mean	Lower	Upper
0 to 2	WA, ID, NV, UT, CO,AZ, NE, IA, WI, MN, NY, NH, VT, NJ, OR, NM, KS, IL, IN, OH, PA, WV (N=22)	Early detection removal, invasion prevention, and elimination	2010-2011	139	483	22.4%	NA	NA	NA	NA	NA	NA
			2012-2013	182	440	29.3%	0.16	0.13	0.19	0.18	0.12	0.25
			2014-2015	176	446	28.3%	0.05	0.03	0.07	0.15	0.10	0.21
			2016-2017	131	491	21.1%	0.01	0.00	0.02	0.27	0.21	0.34
3	MO, TN, VA, KY, MI (N=5)	Locate undetected populations, minimize damage	2010-2011	149	290	33.9%	NA	NA	NA	NA	NA	NA
			2012-2013	140	299	31.9%	0.07	0.04	0.1	0.2	0.14	0.27
			2014-2015	216	223	49.2%	0.26	0.21	0.31	0.01	0	0.05
			2016-2017	247	192	56.3%	0.18	0.13	0.23	0.04	0.02	0.08
4 to 5	CA, TX, OK, AR, LA, MS, AL, GA, SC, NC, FL (N=11)	Reduce populations, minimize damage	2010-2011	942	102	90.2%	NA	NA	NA	NA	NA	NA
			2012-2013	988	56	94.6%	0.43	0.34	0.53	0	0	0
			2014-2015	1005	39	96.3%	0.30	0.20	0.43	0	0	0
			2016-2017	1010	34	96.7%	0.16	0.08	0.30	0	0	0
All	N=38		2010-2011	1230	875	58.4%	NA	NA	NA	NA	NA	NA
			2012-2013	1310	795	62.2%	0.14	0.11	0.18	0.05	0.03	0.07
			2014-2015	1397	708	66.4%	0.13	0.10	0.17	0.02	0.01	0.04
			2016-2017	1388	717	65.9%	0.06	0.04	0.09	0.03	0.02	0.05

Supplementary Figures

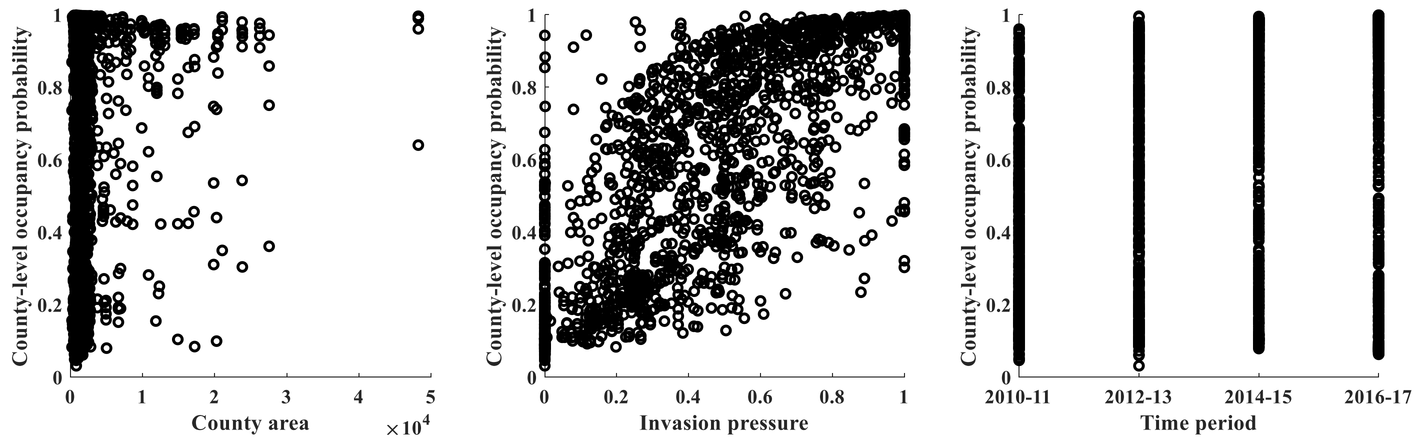

Figure S1. Scatterplot of generalized linear mixed model predictions as a function of main effects. Note the fitted model showed that the three-way interaction between county area, invasion pressure, and time period was significant (p = 0.0041, Table S5), emphasizing that any effects of county area on occupancy probability depend on invasion pressure (how surrounded that county is by other occupied counties) and time period. This suggests that the effects of county area in affecting detection probability are weak (see the relationship on the plot on the left).

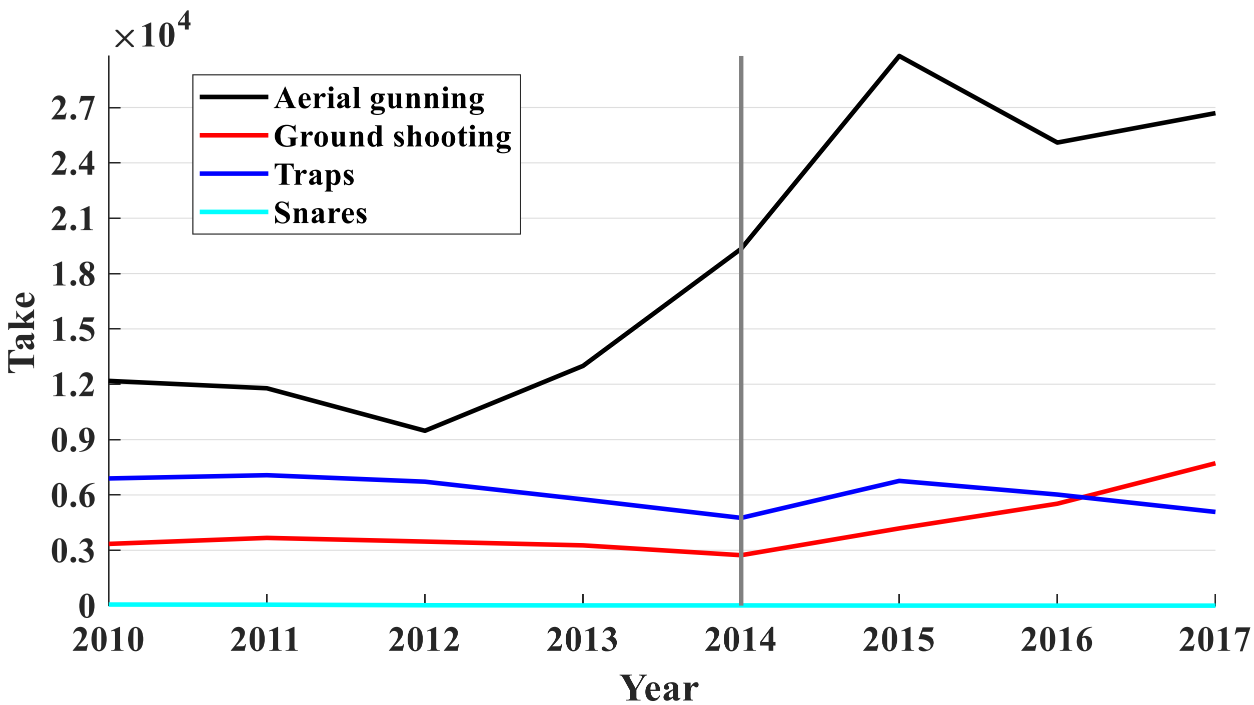

Figure S2. Temporal trends in removal intensity by method. Total number of pigs removed during each year is plotted for each removal method. The vertical grey line indicates the first year of the program. This plot compares the temporal removal intensity across methods.

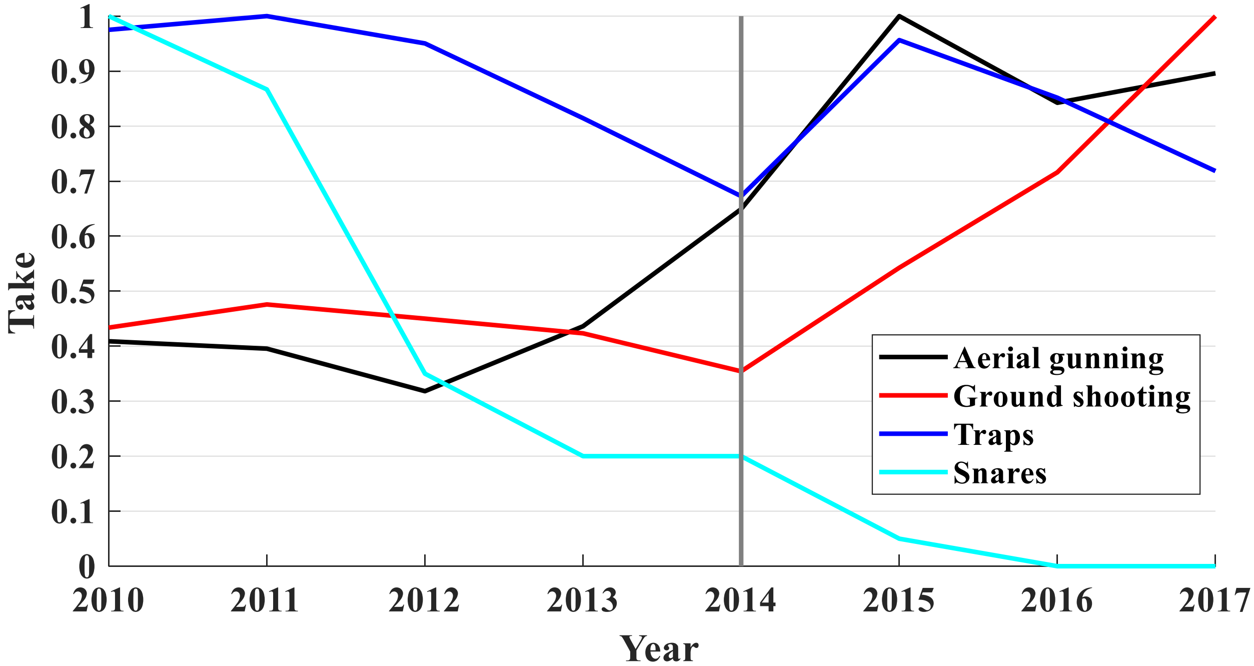

Figure S3. Temporal trends in relative removal intensity by method. For each method, total number of pigs removed per year was rescaled relative to the maximum number of pigs removed in any one year. This plot shows the temporal trends within each method.

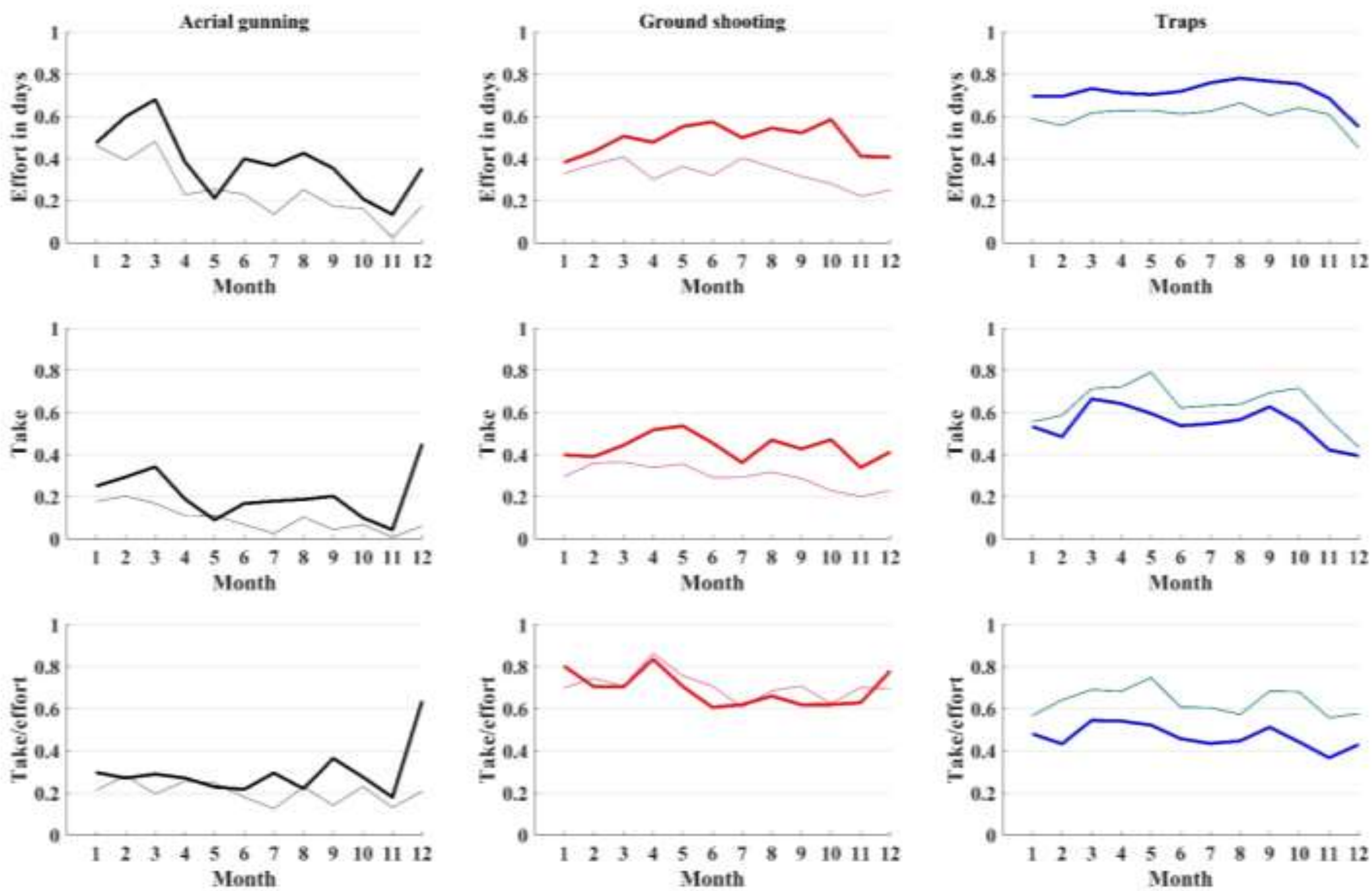

Figure S4. Seasonality in removal intensity. Monthly counts of effort days and number of pigs removed for 3 different removal methods. Data are rescaled to be proportions of the total. Each line represents the mean for 4 years of data. Thin lines are 2010-2013 (pre-program), thick lines are 2014-2017 (during program). Top: proportion of total number of effort days. Middle: proportion of total number of pigs removed. Bottom: proportion of total take/effort ratios.

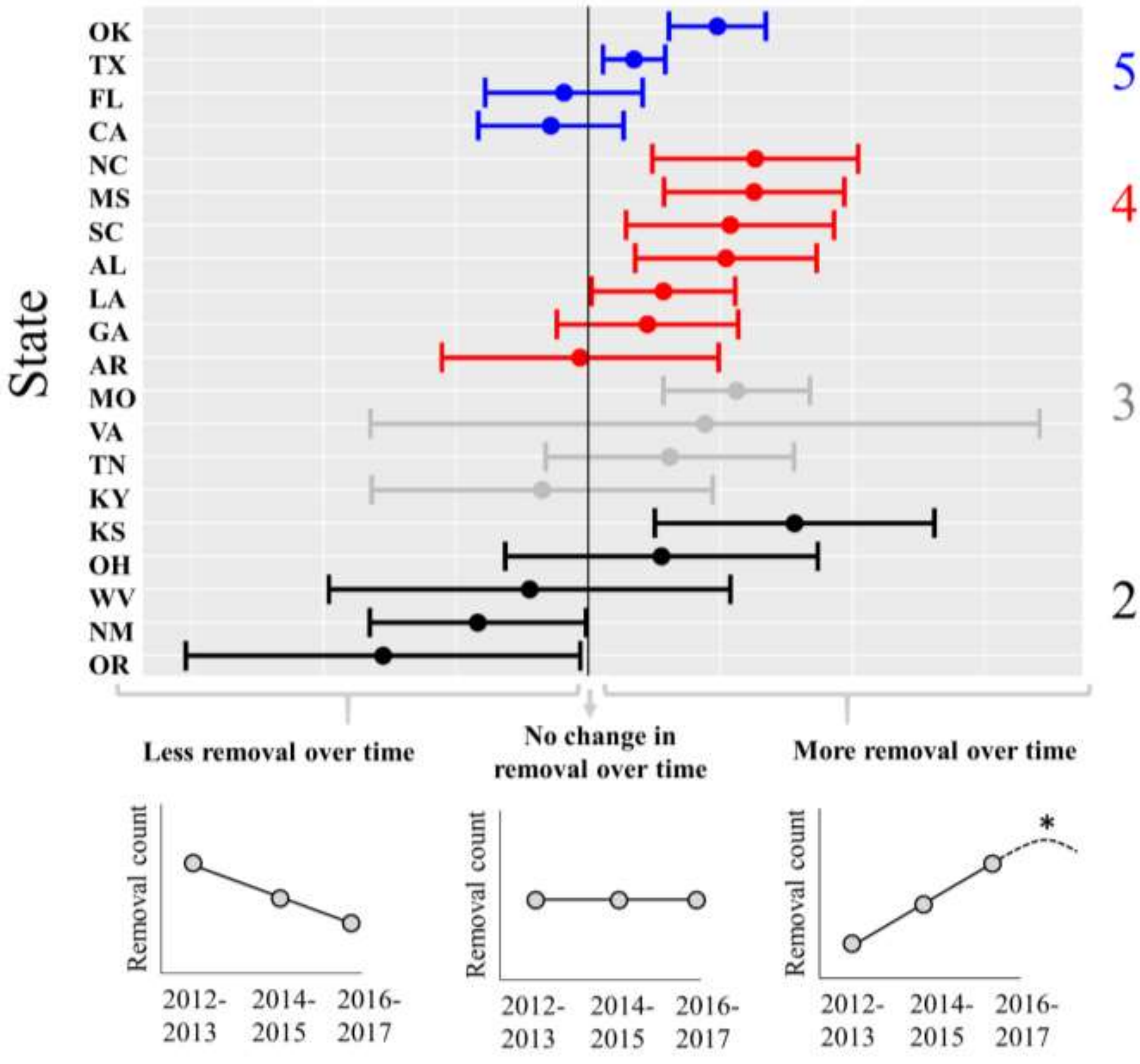

Figure S5. Coefficients for the slope of the relationship between the three time periods and removal counts by state. Error bars are the 95% confidence intervals of the slope estimate. Numbers on the right indicate state funding level classification during the first year of the program (2014). Schematic below the plot explains the meaning of negative and positive slopes relative to program objectives. The asterisk (*) indicates a theoretical threshold where removal rates may begin to decline once they are high enough to start strongly affecting abundance.

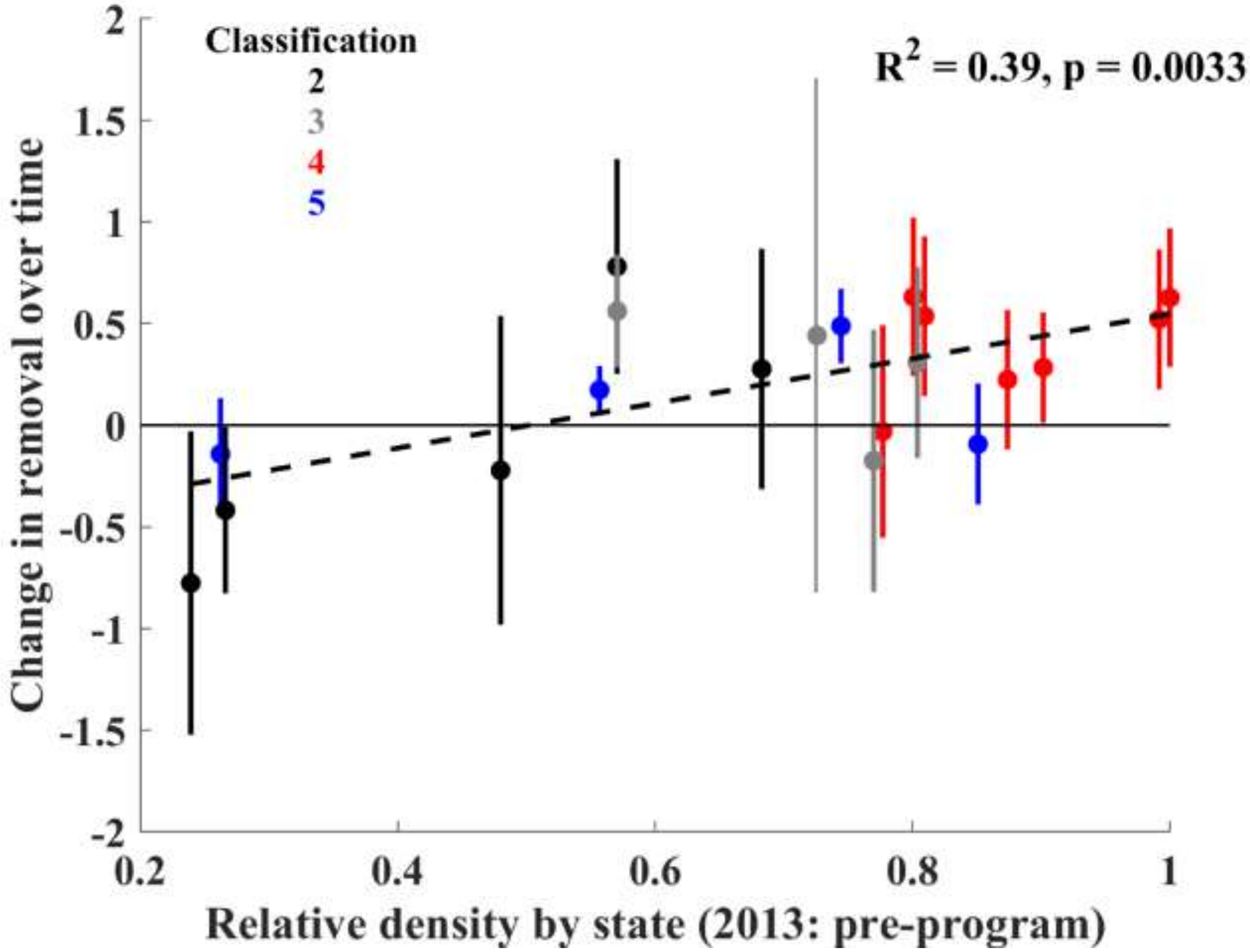

Figure S6. Scatterplot of removal intensity slopes to pre-program estimates of pig density in each state. Error bars are the 95% confidence intervals of the slope estimate. Slope for each state is color-coded by its program classification in the first year of the program (2014). The horizontal dotted line shows no change in removal intensity as the program progresses. The dashed line indicates the predicted slope of the regression of the mean slope estimates (points) against state-level relative density estimates (X-axis). The slope was significantly positive with $p < 0.05$.