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Anna M. Mangan

USDA APHIS National Wildlife Research Center, anna.mangan@usda.gov

Antoinette J. Piaggio

USDA APHIS National Wildlife Research Center

Michael J. Bodenchuk

USDA Animal and Plant Health Inspection Service (APHIS)

Courtney F. Pierce

USDA APHIS National Wildlife Research Center

Timothy J. Smyser

USDA APHIS National Wildlife Research Center

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Research Article

Rooting Out Genetic Structure of Invasive Wild Pigs in Texas

ANNA M. MANGAN,¹ *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA*

ANTOINETTE J. PIAGGIO, *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA*

MICHAEL J. BODENCHUK, *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, P.O. Box 690170, San Antonio, TX 78269, USA*

COURTNEY F. PIERCE, *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA*

TIMOTHY J. SMYSER, *United States Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services, National Wildlife Research Center, 4101 LaPorte Avenue, Fort Collins, CO 80521, USA*

ABSTRACT Invasive wild pigs (*Sus scrofa*), also called feral swine or wild hogs, are recognized as among the most destructive invasive species in the world. Throughout the United States, invasive wild pigs have expanded rapidly over the past 40 years with populations now established in 38 states. Of the estimated 6.9 million wild pigs distributed throughout the United States, Texas supports approximately 40% of the population and similarly bears disproportionate ecological and economic costs. Genetic analyses are an effective tool for understanding invasion pathways and tracking dispersal of invasive species such as wild pigs and have been used recently in California and Florida, USA, which have similarly long-established populations and high densities of wild pigs. Our goals were to use molecular approaches to elucidate invasion and migration processes shaping wild pig populations throughout Texas, compare our results with patterns of genetic structure observed in California and Florida, and provide insights for effective management of this invasive species. We used a high-density single nucleotide polymorphism (SNP) array to evaluate population genetic structure. Genetic clusters of wild pigs throughout Texas demonstrate 2 distinct patterns: weakly resolved, spatially dispersed clusters and well-resolved, spatially localized clusters. The disparity in patterns of genetic structure suggests disparate processes are differentially shaping wild pig populations in various localities throughout the state. Our results differed from the patterns of genetic structure observed in California and Florida, which were characterized by localized genetic clusters. These differences suggest distinct biological and perhaps anthropogenic processes are shaping genetic structure in Texas. Further, these disparities demonstrate the need for location-specific management strategies for controlling wild pig populations and mitigating associated ecological and economic costs. © 2021 The Wildlife Society. This article has been contributed to by US Government employees and their work is in the public domain in the USA.

KEY WORDS feral swine, invasive species, population genetic structure, SNP, *Sus scrofa*, Texas, wild pig.

Invasive wild pigs (*Sus scrofa*) are recognized as among the most destructive invasive species in the world, damaging natural and human-dominated systems (Lowe et al. 2000, Doherty et al. 2016). We use the term wild pigs, also referred to as feral swine or wild hogs among other names, to refer to any free-living member of *Sus scrofa*, regardless of their origins from domestic pigs, wild boar, or hybrids of the 2 lineages (Keiter et al. 2016, Smyser et al. 2020). With invasive populations established in North America, South America, Africa, Australia, and remote Oceanic and Asian islands, wild pigs have one of the largest geographic distributions of all terrestrial mammals (Oliver 1993,

Barrios-Garcia and Ballari 2012). Across this global scale, wild pigs negatively influence biodiversity and ecosystem function. Doherty et al. (2016) report that pigs are among the top 5 invasive mammalian predators contributing to species decline and extinction, with direct negative effects on endangered species such as loggerhead sea turtles (*Caretta caretta*; Engeman et al. 2019) and golden-checked warblers (*Setophaga chrysoparia*; International Union for Conservation of Nature [IUCN] 2019). Furthermore, wild pigs alter habitat through their rooting and wallowing behaviors and have cascading effects on ecosystems (Crooks 2002). Physical damage to plants and soils has been reported to alter soil chemistry and increase nutrient leaching, increase erosion, and reduce species diversity among plants and vertebrates (Singer et al. 1984, Bankovich et al. 2016, Ivey et al. 2019). Within human-dominated

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¹E-mail: anna.mangan@usda.gov

landscapes, wild pigs damage numerous agricultural crops such as potatoes, oats, corn, sugarcane, and sorghum and depredate livestock, particularly newborn sheep, goats, and cattle (Seward et al. 2004, Barrios-Garcia and Ballari 2012). Additionally, wild pigs damage lawns, gardens, trees, and structures such as fences (U.S. Department of Agriculture [USDA] 2019) and have disturbed irreplaceable artifacts at archaeological sites (Engeman et al. 2013). Finally, wild pigs carry pathogens, such as *Brucella* spp., influenza A, and pseudorabies, that pose risks to the health of humans and domestic animals (Bevins et al. 2014).

Free-ranging pig populations have been present in the contiguous United States since first introduced with the Spanish expedition led by Hernando de Soto in 1539 (Mayer and Brisbin 1991, Zadik 2005). The de Soto expedition was provisioned with a large herd of pigs, shepherded behind the expeditionary force as a mobile food supply during their exploration of the Florida peninsula and what would become the southeastern United States (Zadik 2005). The de Soto herd ultimately gave rise to wild populations and managed herds throughout the region as a result of animals that escaped or were stolen by or traded with Indigenous peoples (Zadik 2005). Following the establishment of these initial populations, the number and distribution of wild pig populations likely continued to expand as a consequence of the use of traditional husbandry practices for pig rearing (i.e., the seasonal release of pigs into forested ecosystems to fatten on fallen mast), which remained a common practice until the mid-1900s (Mayer and Brisbin 1991, White 2011). Subsequently, as interest in recreational hunting grew through the early twentieth century, wild boar were introduced from native populations in Europe to increase the hunting appeal of pigs, ultimately augmenting and interbreeding with feral populations that had descended directly from domestic pigs (Mayer and Brisbin 2009, Smyser et al. 2020). Over the past hundred years, through processes of range expansion and natural and anthropogenic gene flow, contemporary wild pig populations in the United States have come to overwhelmingly represent hybrids of Western domestic breeds and wild boar from Europe (Smyser et al. 2020).

Following initial introductions, self-sustaining populations of wild pigs remained largely restricted to California, Texas, and the southeastern United States through the 1980s. Since that time, however, rapid population growth has led to the establishment of populations in as many as 38 states with abundance in the United States estimated at 5–6.9 million animals (Bevins et al. 2014, Lewis et al. 2019). This rapid expansion has been facilitated by the animal's generalist diet, high fecundity, and ability to adapt and thrive in a variety of natural- and human-dominated landscapes (Oliver 1993, Taylor et al. 1998, Ballari and Barrios-García 2014, Bevins et al. 2014, Lewis et al. 2017). Deliberate introduction of wild pigs by humans into uninvaded landscapes, presumably for the creation of new populations for hunting, has also contributed to recent range expansion and perpetuation of wild pig populations (Tabak et al. 2017, Hernández et al. 2018, Smyser et al. 2020). The expanding

distribution of wild pigs in the United States has been accompanied by growing ecological, health, and economic consequences, mirroring the detrimental effects documented throughout the global range. For example, McClure et al. (2018) estimated that more than 123 species protected under the United States' Endangered Species Act of 1973 are directly imperiled by the effects of wild pigs. Further, wild pig damage is economically burdensome with annual costs for the United States estimated at \$1.5 billion annually (Pimental 2007), although this figure is acknowledged to represent an underestimate of the cost of wild pigs (Anderson et al. 2016, McKee et al. 2020).

Texas, in particular, has a long history with wild pigs and bears significant costs associated with their expanding distribution (Anderson et al. 2019). Similar to the introduction patterns throughout much of the continental United States, domestic pigs were brought to Texas as early as 1542 by the de Soto expedition, with feral populations later interbreeding with wild boar introduced from Europe throughout the twentieth century (Mayer and Brisbin 1991). Today, Texas supports more wild pigs than any other state, about 40% of the United States population, with abundance estimated at 2.5 million animals and populations established in all but 1 of the state's 254 counties (Timmons et al. 2012, Lewis et al. 2019, USDA 2019). Biological and anthropogenic factors make wild pig management in Texas challenging. Their vast spatial extent and abundant populations strain management resources and make complete elimination unrealistic as a management objective. Further, current state and federal regulations enable the development of industries associated with wild pigs, such as hunting-related services or the sanctioned collection, slaughter, and processing of wild pig meat for consumption in the human food chain. These various economies incentivize the continued presence of wild pigs despite damages incurred by agricultural producers and other landowners.

Within the context of invasive species control, genetic analyses are an effective tool to help guide management action (Browett et al. 2020, Pepin et al. 2020). For example, genetic analyses can elucidate invasion pathways and provide an understanding of patterns of dispersal and expected rates of range expansion (Le Roux and Wicczorek 2009). Genetic structure assessments have also been used to predict how invasive species may respond to eradication efforts (e.g., recolonization, source-sink dynamics), thus informing the scale at which management actions should be conducted (Abdelkrim et al. 2005, Hopken et al. 2015). Understanding population genetic structure is a precursor to addressing many wild pig management questions and can offer reliable insights into invasion processes and provide a useful tool for guiding management and policy. At a national scale, California, Florida, and Texas represent 3 anchor points for historical wild pig populations and contemporary wild pig management in these states continues to pose significant challenges. Furthermore, each of these states are predicted to have moderate (6 individuals/km²) to high (>11 individuals/km²) population densities of wild pigs into the future (Lewis et al. 2017). Genetic structure of wild pigs has been

previously described for California and Florida, with anthropogenic influences identified as contributing to local range expansion (Tabak et al. 2017, Hernández et al. 2018). In California, Tabak et al. (2017) determined that populations were structured at fine spatial scales, which was attributed to the matriarchal social structure and limited dispersal capacity of wild pigs (Hampton et al. 2004, Fulgione et al. 2016, Morelle et al. 2016). Further, Tabak et al. (2017) documented evidence of human-mediated translocation of wild pigs with introduction rates positively associated with the number of pig farms and game farms (captive hunting facilities) and emigration rates positively associated with the number of wild pigs harvested by licensed hunters and the number of big game outfitters. Similar to this work, Hernández et al. (2018) described finely structured wild pig populations throughout Florida and further documented the role of human-mediated translocation in the expansion of this invasive species. Although recent genetics studies have addressed the population structure in California (Tabak et al. 2017) and Florida (Hernández et al. 2018), genetic analyses of wild pigs have yet to be conducted for Texas on a similar state-wide scale.

Our goals were to use molecular approaches to describe genetic structure and elucidate the invasion and migration processes shaping wild pig populations throughout Texas, compare our results with patterns of genetic structure observed in California and Florida, and use our results to provide insights for effective management of this invasive species. We predicted wild pigs in Texas would exhibit comparable population structure to that of populations in California and Florida because of their similar introduction histories and contemporary expansions.

STUDY AREA

We conducted our study in Texas from May 2012 to March 2019, with the collection of genetic samples occurring throughout the study period (Table S1, available online in Supporting Information). Texas spans approximately 695,662 km² and includes 10 ecoregions that range in elevation from sea level along the Gulf Prairies and Marshes region to 2,667 m above sea level in the Trans-Pecos region (Gould et al. 1960, Texas Parks and Wildlife Department 2020). Climate, weather, and dominant flora and fauna vary across the ecoregions in our study area. Briefly, according to Texas Parks and Wildlife Department (2020) the state is comprised of the following ecoregions: 1) Piney Woods, which has a humid subtropical climate, average annual rainfall of 914–1,270 mm, and dominant flora of pine (*Pinus* spp.) and pine-hardwood; 2) Gulf Prairies and Marshes, which has a humid subtropical climate with average annual rainfall of 762–1,270 mm, dominant flora of saltgrass (*Distichlis spicata*) marshes, tallgrass prairies, mesquite (*Prosopis* spp.), and oak (*Quercus* spp.), and dominant fauna of migratory birds, fish, and shrimp; 3) Post Oak Savannah, which has a humid subtropical climate, average annual rainfall of 711–1,016 mm, and dominant flora of oak and

grassland; 4) Blackland Prairie, which has a humid subtropical climate, average annual rainfall of 711–1,016 mm, and dominant flora of tallgrass prairie; 5) Cross Timbers, which has a humid subtropical climate with erratic rainfall and dominant flora of tallgrass prairie, savanna, and woodland; 6) South Texas Plains, which has a warm semi-arid climate, average annual rainfall of 508–813 mm, and dominant flora of brush such as mesquite; 7) Edwards Plateau, which has a warm semi-arid to humid subtropical climate, average annual rainfall of 381–864 mm, dominant flora of grasslands, juniper (*Juniperus* spp.)-oak, live oak, and savanna; 8) Rolling Plains, which has a cold semi-arid and humid subtropical climate, average annual rainfall of 508–711 mm, and dominant flora of short, mid, and tallgrass prairie, and mesquite; 9) High Plains, which has a cold semi-arid climate, average annual rainfall of 381–559 mm, dominant flora of shortgrass prairie, mesquite, and juniper, and dominant fauna of bison (*Bos bison*), pronghorn (*Antilocarpa americana*), prairie dogs (*Cynomys* spp.), and waterfowl; and 10) Trans-Pecos, which has warm and cold desert and warm and cold semi-arid climates, average annual rainfall of <305 mm, dominant flora of creosote (*Larrea tridentata*)-tarbush (*Flourensia cernua*) desert scrub, desert grassland, yucca (*Yucca* spp.) and juniper savanna, pinion pine (*Pinus edulis*), and oak. Additionally, dominant fauna across the state includes white-tailed deer (*Odocoileus virginianus*), migratory birds, and waterfowl (Texas Parks and Wildlife Department 2020). Primary land uses are farming, ranching, and timber (Texas Parks and Wildlife Department 2020). Current efforts to map the distribution of wild pigs suggest all but 1 of the 254 counties in Texas (El Paso County) support wild pig populations (USDA 2019). Although habitat suitability can be influenced by a number of abiotic and biotic factors, the majority of the state is occupied by wild pigs with very little potential for increases in abundance or distribution because almost all suitable habitat is occupied (Lewis et al. 2017, 2019; Snow et al. 2017).

METHODS

Sampling and DNA Extraction

We obtained a variety of sample types (i.e., hair, pinna, and kidney) collected across 101 Texas counties from euthanized wild pigs that were sampled ancillary to population reduction and damage mitigation conducted by the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service (APHIS) Wildlife Services (WS) Feral Swine Damage Management Program between May 2012 and March 2019 (Table S1). We submitted samples to the National Feral Swine Genetic Archive (USDA APHIS WS National Wildlife Research Center) for analysis along with corresponding metadata, which included sex, age class, date of collection, and collection location (county and spatial coordinates rounded to the hundredth of a degree to protect the anonymity of private landowners while providing spatial accuracy within ~1.1 km). Given that genetic

samples were collected secondarily to legally authorized control of wild pigs, sample collection was exempted from Institutional Animal Care and Use Committee review.

We extracted genomic DNA with a commercially available magnetic bead recovery kit (MagMax, Thermo Fisher Scientific, Waltham, MA, USA) using the MagMax Processor (Applied Biosystems, Waltham, MA, USA). We then genotyped samples using the GeneSeek Genomic Profiler for Porcine HD (GeneSeek, a Neogen Corporation, Lincoln, NE, USA; Illumina, San Diego, CA, USA), a commercially available genotyping array with 62,128 biallelic, autosomal single nucleotide polymorphisms (SNP) mapped to the Sscrofa 11.1 genome assembly (Warr et al. 2019). We used SNP & Variation Suite version 8.8.3 (Golden Helix, Bozeman, MT, USA) to implement standard quality control measures for SNP data. Specifically, we pruned loci with low call rates (<95%) and minor allele frequencies (MAF) < 0.05 (11,800 loci pruned), then removed individuals with low genotype call rates (<95%; 25 samples pruned) and finally, evaluated linkage disequilibrium (LD) among markers and pruned closely linked loci ($r^2 > 50\%$; window size = 50, window increment = 5) within chromosomes (20,505 loci pruned).

Population Structure Analysis

We used 2 independent approaches to describe population genetic structure. Initial evaluation of genetic relatedness relative to geographic distance demonstrated patterns of isolation by distance (Mantel test conducted with R package *vegan*; Oksanen et al. 2013, R Core Team 2019) with relationships visualized by fitting a loess curve to a scatterplot with the R package *msir* (Scrucca 2011; Table S2 and Fig. S1, available online in Supporting Information). Accordingly, we first used the R package *conStruct* version 1.0.4 to describe patterns of genetic structure (Bradburd et al. 2018); *conStruct* explicitly accounts for isolation by distance to avoid erroneously delineating discrete clusters from a continuous pattern of genetic variation (Bradburd et al. 2018). A limitation of *conStruct* is that it is computationally intensive, with run times that are prohibitive for analyses of datasets with large sample sizes. The method, however, allows for collapsing samples within a sampling location for analysis of pooled allele frequencies under a rationale that samples collected from a given location represent replicates in the estimation of local allele frequencies. Therefore, we used R package *dbSCAN* (Hahsler et al. 2019), a density-based spatial clustering method to assign samples to a collapsed sampling location if they are proximate to other samples from that location. Given a minimum number of samples per collapsed location (option *minPts* = 2) within a specified radius (epsilon neighborhood radius = 0.1), we defined 110 collapsed locations with a range in the number of samples from 2 to 38; we analyzed outlier points ($n = 45$) as individual locations, collectively representing 155 sampling locations for *conStruct* analysis (Table S3, available online in Supporting Information). We then calculated mean allele frequencies for each of the 155 sampling locations and used the centroid of samples within

a collapsed sampling location for spatial analysis. We evaluated genetic clusters (K) from 2 to 13 using 20,000 iterations (10,000 burn-in iterations followed by 10,000 sampling iterations), assessing model convergence and performance for each K across 3 chains. To select the most informative model of K , we evaluated several elements of the *conStruct* output. Under the assumption that multiple independent runs should converge on the same results, we examined the log posterior density and parameter estimates over iterations to evaluate model convergence. For each value of K , we assessed the layer contributions to identify clusters with statistical support but only minor biological support by multiplying within-cluster covariance with the admixture proportions of samples in that cluster to calculate the relative contribution of each cluster to total covariance (Bradburd et al. 2018). Given that large layer contributions are present when many samples draw large amounts of admixture from a cluster or if the layer has a very large within-cluster covariance, we interpreted models that included layers with low contributions (e.g., <0.1) as having poor fit for the genetic structure of the data. Finally, under the assumption that genetic clusters should be geographically cohesive, we assigned each collapsed sampling location to a genetic cluster based on their ancestry proportions (Q); assigning the collapsed sampling locations to the cluster from which they had the strongest association) and mapped their distribution (ArcMap version 10.6, Esri, Redlands, CA, USA) to qualitatively evaluate the spatial relationships within and among genetic clusters and identify levels of geographic cohesion under alternative values of K (Puechmaille 2016).

Second, we used *ADMIXTURE* (Alexander et al. 2009) to evaluate K from 2 to 30. *ADMIXTURE* implements the well-established, genetic model-based clustering approach used in *STRUCTURE* (Pritchard et al. 2000) but casts the algorithm in a maximum likelihood framework to increase computational efficiency as required for analysis of high-density SNP arrays (Libiger and Schork 2013). We used 3 methods to guide selection of the most informative value of K . One, we used *ADMIXTURE*'s cross-validation procedure to evaluate relative support for different values of K . Implementing a random seed, we conducted 10 *ADMIXTURE* runs for each K from which we calculated the mean and standard deviation of the cross-validation error. We interpreted models with lower mean cross-validation error and less variation among runs as having better fit for the genetic structure within the data. Two, we evaluated the strength of association of samples to the delineated clusters under the rationale that more informative models will be characterized by individuals strongly associated with a given cluster as opposed to individuals associated with many clusters (i.e., heavily admixed; Pritchard et al. 2000). Specifically, we identified the maximum association (Q_{max}) of each individual to the K clusters, estimated by *ADMIXTURE* as the ancestry fraction in the Q matrix (Alexander et al. 2009). We then evaluated mean Q_{max} values over competing models of K , favoring models in which individuals were strongly associated with genetic clusters (i.e., high Q_{max} values) over those in which

individuals were highly admixed (i.e., low Q_{max} values), and visualized patterns of association among K clusters with bar plots generated using STRUCTURE PLOT V2.0 (Ramasamy et al. 2014). Three, we assigned individuals to genetic clusters based on their Q_{max} values and mapped their distribution to qualitatively evaluate the spatial relationships and identify levels of geographic cohesion under alternative models of K .

Following the identification of the most informative delineation of genetic structure, we used the R packages HierFstat to calculate global and pairwise F_{ST} and StAMPP to calculate Nei's genetic distance among all pairwise combinations of K clusters (Goudet 2005, Pembleton et al. 2013). To visualize the patterns of genetic association among the K genetic clusters, we then constructed a neighbor-joining tree with SplitsTree4 (Huson and Bryant 2006) by linking the least distant pair of clusters, as described with Nei's genetic distance, followed by successively more distant clusters. Finally, we used the R package adegenet to perform a principal component analysis (PCA; Jombart 2008), treating genotypes as multivariate data unconstrained by a specific genetic model. The use of PCA to describe genetic structure is recognized to provide a complementary perspective to clustering analyses that is better suited for describing continuous patterns of genetic structure as opposed to discrete genetic clusters, which is more effectively delineated with clustering analyses (McVean 2009, Petkova et al. 2016). We plotted pairwise combinations of principal components (PCs) to visualize genetic structure among the samples.

RESULTS

We sampled 767 wild pigs distributed across 101 counties in Texas. After implementing standard quality control measures for both the retention of loci and individual genotypes, our dataset consisted of 742 wild pigs genotyped with 29,823 loci.

Visual inspection of the log posterior density and parameter estimates from conStruct showed similar output across multiple chains for $K=2$ to 13, suggesting acceptable model convergence using 20,000 iterations. Both clusters within $K=2$ had approximately equal layer contribution values (Fig. S2, available online in Supporting Information). Higher models of K contained ≥ 1 clusters with weak layer contribution (i.e., values < 0.1), ranging from 33% of clusters ($K=3$) to 86% of clusters ($K=6$), which is indicative of poor model performance. In evaluating spatial patterns of genetic clusters, $K=2$ bifurcated the state along a north-south gradient (Fig. 1A). Increasing values of K were characterized by the addition of numerically small clusters with few, weakly associated sampling locations. Although these outliers did not group into clearly defined clusters, they demonstrated weak but interesting patterns, namely highly admixed pockets of collapsed locations along the east and west borders of the state. Based on layer contribution results and spatial patterns of clustering, we concluded $K=2$ was the most informative model for describing genetic structure with an explicit spatial component (Figs. 1A and 2A).

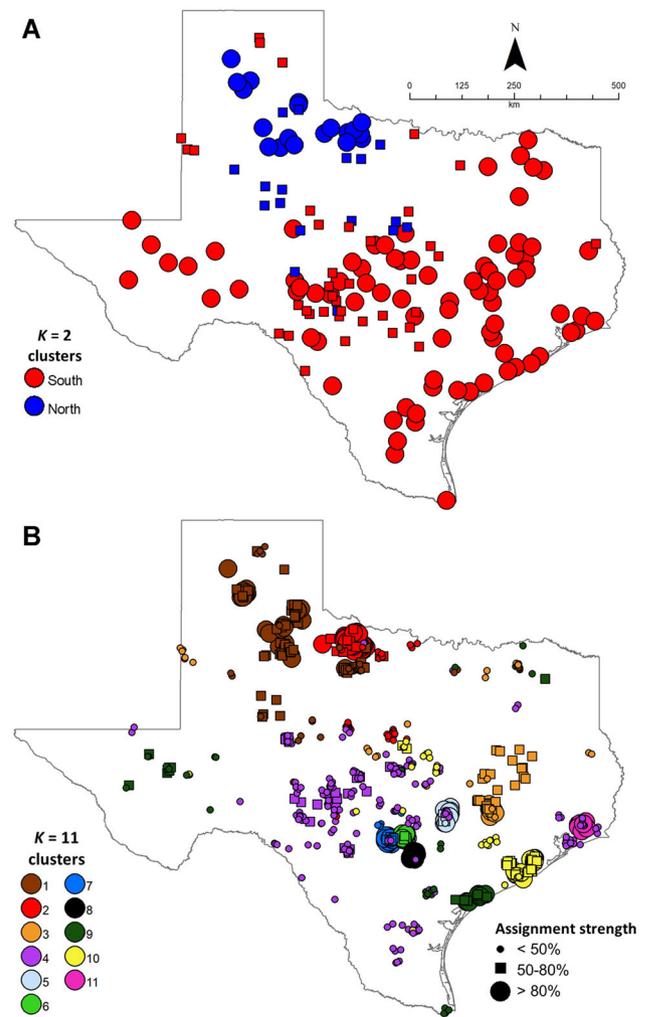


Figure 1. Geographic distribution of invasive wild pigs collected across 101 counties in Texas, USA, May 2012–March 2019. A) Centroid of 155 collapsed sampling locations pooled with dbSCAN (Hasler et al. 2019) across 2 genetic clusters (K) as delineated using conStruct. B) Sample collection locations of 742 individuals across 11 genetic clusters as delineated using ADMIXTURE. For improved visualization, coordinates were jittered with the addition of a random number ($\bar{x} = 0$, $SD = 0.045$ degrees). Point colors correspond to assigned clusters and point size and shape correspond to the maximum association (Q_{max}) of each individual (or collapsed sampling location) to its assigned cluster.

The cross-validation error returned from ADMIXTURE decreased asymptotically to $K=22$, after which the cross-validation error was relatively flat but variable for higher values of K (Fig. S3, available online in Supporting Information). Standard deviation of the cross-validation error calculated across 10 runs for each K was consistently small from 2 to 14 but increased for higher values of K , indicative of declining model performance. Distribution of Q_{max} values varied across K models, with average Q_{max} ranging from 0.55 ($K=6$) to 0.85 ($K=2$; Fig. S4, available online in Supporting Information). In evaluating spatial patterns of genetic clusters, $K=2$ bifurcated the state along a north-south gradient. Both clusters within $K=2$ were well-resolved, with $> 70\%$ of individuals showing Q_{max} values > 0.80 (Fig. 2B). From within these 2 broad regional

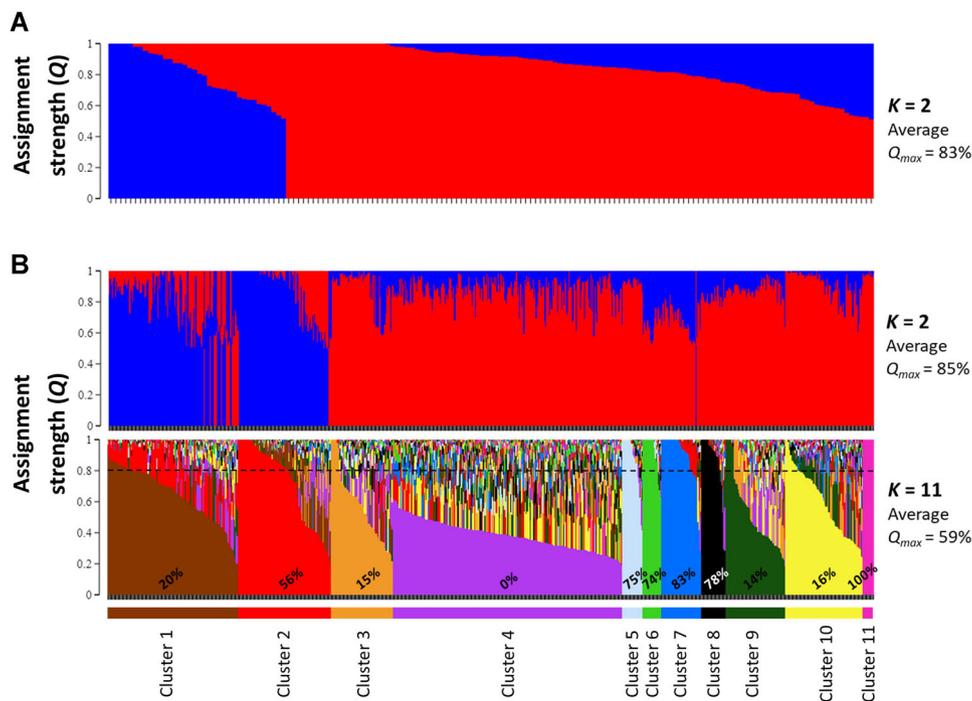


Figure 2. Bar plots generated with STRUCTURE PLOT (Ramasamy et al. 2014) representing the strength of assignment (Q) to clusters for various models of genetic structure (K) of invasive wild pigs collected across 101 counties in Texas, USA, May 2012–March 2019. A) The most informative model of genetic structure, $K=2$, as derived from the conStruct analysis. We calculated the proportion of assigned membership using the mean allele frequency for 155 collapsed sampling locations, which were pooled with dbSCAN (Hasler et al. 2019). B) Bar plots for 742 wild pigs as delineated with ADMIXTURE for $K=2$ and 11; numeric cluster identifiers for $K=11$ are presented below the plots. A dashed line in the $K=11$ panel marks assignment strength of 0.8, and the percent of individuals per cluster with strong membership assignment ($Q > 0.8$) are displayed at the base of each cluster. Individuals in the $K=2$ plot are displayed in the same order as the $K=11$ plot. Both the conStruct (A) and ADMIXTURE (B) $K=2$ bar plots illuminate an early north-south bifurcation trend seen through increasing values of K in both analyses. The average maximum association (Q_{max}) of individuals to their assigned cluster is shown at the right for reference.

groups, more geographically restricted, distinct clusters emerged with increasing values of K . There was a consistent pattern from $K=4$ to 30 in which a single cluster was poorly characterized, with no individuals strongly associated with the specified cluster. We designated this outlier cluster across models of K as other, a group without strong biological meaning; however, the remaining clusters within a given model of K from 4 to 30 remain biologically informative. Based on these cross-validation results, Q_{max} values, and spatial patterns, we concluded $K=11$ was the most informative model for describing genetic structure and guiding management within Texas given the available data (Fig. 1B). With $K=11$, 192 individuals (26%) assigned strongly to a genetic cluster ($Q_{max} > 0.8$) with an overall average Q_{max} of 0.59 (Figs. 2B and S4).

Based on the delineation of individuals among clusters with $K=11$, the neighbor-joining tree further elucidated patterns from the ADMIXTURE analysis. Specifically, the northernmost clusters (1 and 2) were distinct, grouped tightly together, and corroborated the north-south bifurcation observed with $K=2$ (Figs. 2 and 3). Further, the most divergent clusters were 5, 6, 7, 8, and 11, which were well-resolved clusters with high Q_{max} values (Figs. 1B and 2B). Clusters 3, 4, 9, and 10 also grouped together as expected, given the broad spatial distribution and spatial overlap observed (Fig. 1B). Pairwise F_{ST} results reflected similar patterns of structure and differentiation with a mix of

genetically distinct and similar clusters (Table S4, available online in Supporting Information; min. $F_{ST}=0.026$; max. $F_{ST}=0.234$), whereas global F_{ST} remained moderate ($F_{ST}=0.103$). Additionally, PCA corroborated the patterns of genetic structure resolved with model-based approaches (i.e., ADMIXTURE and conStruct). In particular, relationships among the modeled clusters illustrated grouping of the northernmost clusters (1 and 2) and genetically distinct clusters (e.g., 7), which distinctly separate into unique PCA space (Fig. 4).

DISCUSSION

At the broadest scale, with the least resolution (i.e., $K=2$), we identified a north-south bifurcation of wild pigs in Texas. When we interpret higher models of genetic structure (i.e., $K=11$), however, biologically meaningful clusters are revealed and provide important insights for management. Genetic clusters of wild pigs demonstrated 2 distinct patterns: weakly resolved, spatially dispersed clusters in contrast with well-resolved, spatially localized clusters. The disparity in patterns of genetic structure suggests distinct processes of connectivity and isolation are shaping wild pig populations throughout the state in which some populations are structured through patterns of isolation by distance, whereas others appear to reflect founder effects and drift. The differential biological processes shaping genetic clusters throughout Texas will require the development of

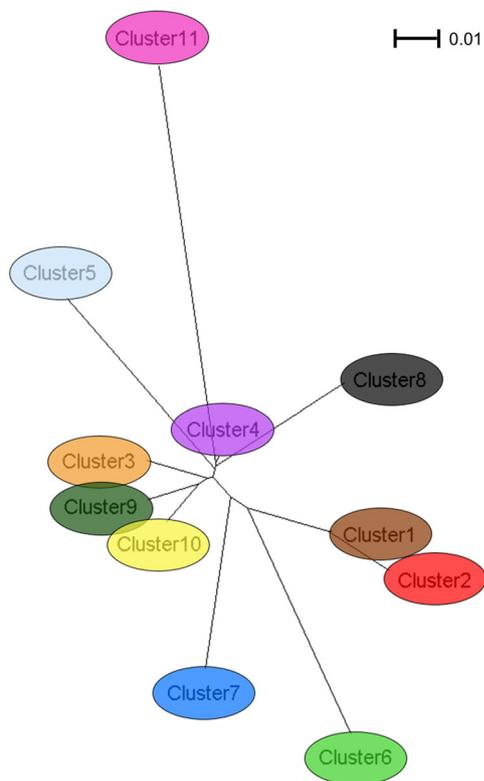


Figure 3. Neighbor-joining tree generated with SplitsTree4 (Huson and Bryant 2006) representing the model of genetic clustering (K) = 11 of 742 invasive wild pigs from 101 counties in Texas, USA, collected May 2012–March 2019 as delineated with ADMIXTURE. The relational tree is constructed by linking genetically similar pairs of clusters, followed by successively more distant clusters. Distances between clusters, based on the scale bar, represent pairwise genetic associations estimated with Nei's genetic distance.

location-specific management strategies for effective wild pig control and damage mitigation. Further, the patterns of genetic structure resolved for Texas differed from patterns observed in California and Florida, suggesting that there are regional differences in processes of invasion and connectivity across landscapes (Tabak et al. 2017, Hernández et al. 2018).

All clusters described within the Texas landscape appeared to be hierarchically structured with clusters differentiated between north (ADMIXTURE clusters 1 and 2, aligning with conStruct northern delineation) and south (ADMIXTURE clusters 3–11, aligning with conStruct southern delineation). This differentiation mirrors historical patterns of expansion of wild pigs in Texas. Early introductions established feral populations in southern Texas, whereas wild pig populations have become established throughout the state only over the past 40 years (Bevins et al. 2014). Northward expansion solely due to natural and gradual range expansion would be expected to produce a continuous pattern of isolation by distance as opposed to the discrete north-south division we observed. We therefore hypothesize that the northern clusters could be attributed to a distinct invasion, likely associated with introductions or range expansion from neighboring states. Although there are many documented cases of wild pig transport into and out of Texas, there are no explicit accounts of invasion pressure from the north (i.e., OK or NM; Mayer and Brisbin 1991). Thus, additional research is needed to identify origins of wild pigs in northern Texas.

Large portions of the Texas landscape were encompassed within weakly resolved, spatially dispersed genetic clusters identified with ADMIXTURE, indicative of connectivity

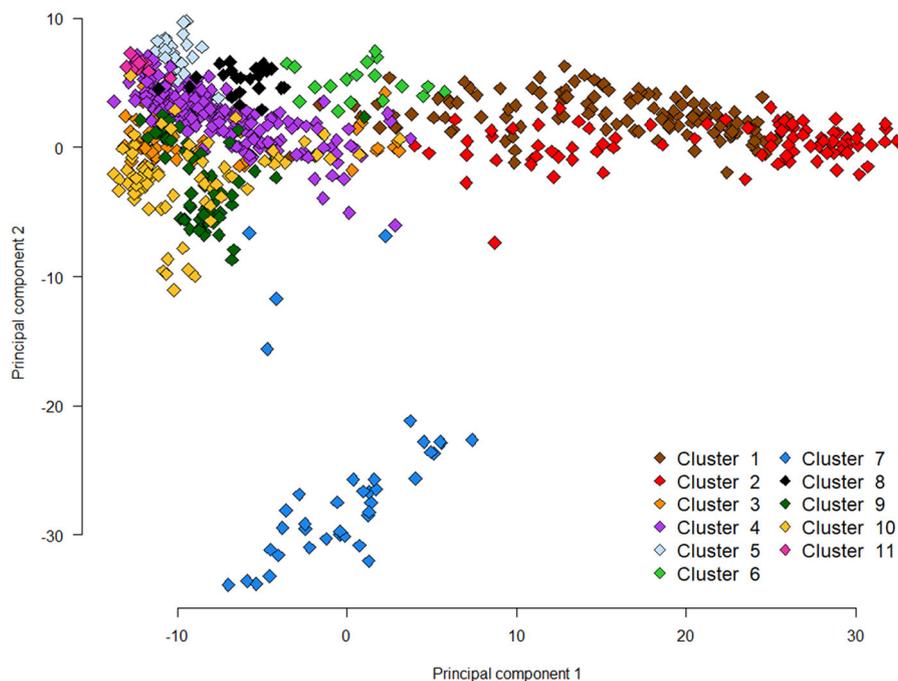


Figure 4. Principal component analysis (PCA) plot generated with adegenet (Jombart 2008) depicting 742 invasive wild pigs across principal component (PC) 1 versus PC2. Samples were collected across 101 counties in Texas, USA, May 2012–March 2019. Point colors correspond to the model of genetic clustering (K) = 11 clusters as delineated with ADMIXTURE. Principal component 1 explains 5% of the variance and PC2 explains 2% of the variance.

that follows patterns of isolation by distance with ongoing gene flow (i.e., clusters 1, 2, 3, 4, 9, and 10; Figs. 1B and 2B). We recognized cluster 4 as a statistical artifact of the clustering analysis and interpret it as an other cluster (i.e., all individuals have Q_{max} values < 0.63) from which we do not draw biological inference. These 6 clusters were characterized by low average Q_{max} values (< 0.72) and contact zones—the sympatric occurrence of individuals that assign to adjacent genetic clusters (Fig. 1B). These weakly resolved, spatially dispersed genetic clusters differed from patterns of genetic structure described previously for wild pigs (Hampton et al. 2004, Spencer and Hampton 2005, Tabak et al. 2017, Hernández et al. 2018). Specifically, wild pig populations are often genetically structured at fine spatial scales with populations organized into discrete genetic clusters—a pattern that has been attributed to the limited dispersal distance of wild pigs relative to their body size and a social structure characterized by female site-fidelity and the formation of matriarchal social groups (i.e., sounders; Hampton et al. 2004, Spencer and Hampton 2005, Tabak et al. 2017, Hernández et al. 2018). One potential hypothesis to explain the different genetic structure observed in Texas is that the rapid expansion of wild pigs since the 1980s has not afforded sufficient time for genetic differentiation to occur. Well-resolved genetic structure, however, has been characterized throughout California and Florida, which have similar introduction histories and widespread populations. Alternatively, a lack of observed genetic structure in Texas could be attributed to inadequate sampling or genetic resolution. Yet with similar sample sizes ($n_{TX} = 742$ vs. $n_{CA} = 736$, $n_{FL} = 482$) and ample genetic resolution afforded with the use of a high-density SNP array (29,823 SNPs vs. 43 microsatellite loci and 52 microsatellite loci for CA and FL, respectively; Liu et al. 2005, Morin et al. 2009, Helyar et al. 2011), we conclude that distinct processes are shaping wild pig populations across these landscapes (Tabak et al. 2017, Hernández et al. 2018).

The higher levels of genetic connectivity necessary to create the spatially diffuse patterns of genetic structure observed in Texas may be attributable to higher levels of dispersal among populations as a result of the saturation of an invaded landscape, larger individual home ranges due to differences in resource availability, or elevated anthropogenic movement of wild pigs. Although our current study did not explicitly evaluate the influence of these attributes on the unique patterns observed for Texas, previous research allows us to evaluate the relative support for these hypotheses. First, we would predict that natal dispersal would be greater in a saturated landscape, such as Texas, relative to California and Florida, states with lower abundance (Lewis et al. 2019). A direct comparison of dispersal distances between these states is not currently possible, however, because research on the natal dispersal of wild pigs in North America has thus far been limited (Gray et al. 2019). Second, differences in the availability and distribution of resources between Texas, California, and Florida may affect individual home range sizes. Trends reported by Kay et al. (2017) suggest wild pigs in Texas move greater distances per

day and have larger home ranges than wild pigs in Florida. Conversely, a more recent study conducted across 10 states reported similar movement patterns of radio-collared wild pigs in Texas, California, and Florida, suggesting the observed regional differences in genetic structure may not be attributable to differences in wild pig movement patterns (Gray et al. 2019). Third, anthropogenic movement of wild pigs in Texas may be sufficient to disrupt the formation of genetic structure generally observed among wild pigs. The weakly resolved, spatially dispersed genetic clusters that dominate much of the Texas landscape make it challenging to identify migrants that could unequivocally be associated with anthropogenic movement. In the absence of well-defined genetic structure, it is possible that individuals are moved hundreds of kilometers and yet are still sampled within the spatial extent of the same broad cluster. A recent study restricted to wild pigs in southern Texas revealed similar patterns of highly admixed populations, which was attributed to multiple introductions and anthropogenic movement (Delgado-Acevedo et al. 2021). Our preliminary isolation by distance analysis (Fig. S1) provided only a single clear example of long-distance migration, identified by high genetic relatedness of an individual from the South Texas Plains to 3 individuals in the western Trans-Pecos region, separated by approximately 600 km. In California, translocation rates were positively associated with anthropogenic predictors related to recreational hunting and related industries (Tabak et al. 2017). Similarly, in Florida, wild pig holding facilities, where wild pigs are temporarily held before being sold for slaughter or released into captive hunting facilities (Florida Department of Agriculture and Consumer Services 2020), served as foci for long-distance immigration. The extent of translocation in both states, however, was sufficiently limited that a clear signal of genetic structure could be resolved, and long-distance migrants could subsequently be identified (Tabak et al. 2017, Hernández et al. 2018). In contrast, in Texas, where industries associated with wild pig hunting and live capture and slaughter of wild pigs are well established, anthropogenic movement has likely contributed to the relative lack of genetic structure.

Accounting for these regional differences in rates of connectivity and associated immigration pressure is important when making large-scale (i.e., nationwide) management decisions regarding this invasive species. Our results unequivocally demonstrate extensive connectivity among wild pig populations in Texas, attributable to either natural connectivity, translocation, or both, yet we lack the population structure to clearly identify sources of migrants. Under any scenario, as abundance increases and wild pigs saturate available habitat, management strategies generally shift from an objective of local elimination to one of population control and damage mitigation (West et al. 2009). Weakly resolved, spatially dispersed genetic clusters that dominated large portions of the landscape will make complete elimination of wild pigs from the spatial extent of these clusters challenging because widespread connectivity poses a persistent reinvasion risk (Delgado-Acevedo

et al. 2013). These vast areas of admixed and spatially dispersed clusters create additional challenges. For example, the control of a foreign animal disease upon introduction in a weakly resolved, spatially dispersed genetic cluster would necessitate the coordination of management action across an extensive area (Brown et al. 2020, Delgado-Acevedo et al. 2021). With genetic patterns demonstrating high rates of connectivity throughout and among these spatially dispersed clusters, policies are needed to limit anthropogenic movement and remove economic incentives that encourage the translocation and release of wild pigs.

In contrast to weakly resolved, spatially dispersed clusters distributed across Texas, analysis with ADMIXTURE revealed 5 well-resolved, spatially localized clusters (clusters 5, 6, 7, 8, and 11; Fig. 1B) that were more akin to the genetic patterns described in California and Florida (Tabak et al. 2017, Hernández et al. 2018). Although these well-resolved clusters were not similarly identified with conStruct, this is not unexpected given that clustering algorithms are influenced by sample size and our use of conStruct represented an analysis of collapsed sampling locations as opposed to individual genotypes (Puechmaile 2016, Lawson et al. 2018). These spatially localized clusters (range = 11 to 39 samples/cluster) were represented by only 1 to 3 sampling locations in the conStruct analysis. Although conStruct is a superior clustering method when accounting for isolation by distance, our results suggest that the loss of fine-scale information necessitates the integration of both analysis approaches when making management decisions. These well-resolved clusters exhibit the greatest divergence in the neighbor-joining tree (Fig. 3), have the strongest cluster assignments (average Q_{max} values >0.85 ; Fig. 2B), and are geographically localized (Fig. 1B). Furthermore, clusters 5, 8, and 11 group tightly together in PCA space, and cluster 7 was clearly differentiated from other clusters along the second PC axis (Fig. 4). These numerically small and spatially limited clusters are likely attributable to similar processes shaping wild pig populations as were described in California and Florida. Hernández et al. (2018) attribute spatially localized clusters in Florida to introductions from distinct genetic sources. Similar novel introductions (e.g., wild boar; Mayer and Brisbin 1991) and subsequent isolation may be occurring in Texas. Finally, distinct genetic signatures may be attributable to isolation as a result of landscape attributes, allowing allele frequencies to drift independently. For example, the majority of individuals from cluster 7 (35 of the 39 wild pigs) were collected on a military training base surrounded by a semi-permeable fence. Fencing and other landscape attributes (i.e., urban development) may limit natural movement and gene flow, thus making clusters susceptible to genetic drift. Well-resolved, localized clusters, especially in isolated areas such as these, are ideal locations for wild pig elimination efforts given that immigration appears to have limited influence on local demographic processes (Barrios-Garcia and Ballari 2012). Accordingly, clusters 5, 6, 7, 8, and 11 could be prioritized for local elimination because a history of genetic isolation suggests there would

be minimal contemporary immigration pressure that might offset population control efforts. Further, the limited spatial extent of these clusters (i.e., 1–3 counties covered by each cluster) would allow for wild pig control to be organized and conducted at a local scale.

Our study addresses a knowledge gap by evaluating genetic attributes of wild pigs throughout Texas, the state with the greatest wild pig abundance, while complementing previous genetic studies conducted elsewhere. Although wild pigs in Texas have a similar history of introduction and contemporary expansion to populations in California and Florida, our results suggest distinct processes are shaping wild pig populations in the state (Tabak et al. 2017, Hernández et al. 2018). We have described large regions in Texas characterized by high levels of genetic connectivity that contrast with isolated pockets of wild pigs and contribute additional genetic evidence of anthropogenic movement. Each of these factors will need to be considered in the development of management plans and allocation of resources for population control. Future research may build upon genetic structure to investigate the influence of policy and management on wild pig damage, movement, and control.

MANAGEMENT IMPLICATIONS

Given the magnitude of the management challenges posed by wild pigs in Texas, the application of genetic tools to elucidate contemporary processes shaping invasive populations can be important in guiding the allocation of limited management resources. Our research demonstrates that the processes of invasions, genetic connectivity, and isolation are influencing the structure of wild pig populations differently in Texas than has been described in California and Florida. Identifying population genetic structure can be a first step for developing efficacious management strategies for the control of wild pigs, as appropriate control measures may vary on both regional and local scales.

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DATA AVAILABILITY STATEMENT

Genotypes for wild pigs included in this study are openly available through the Dryad data repository at <https://doi.org/10.5061/dryad.cz8w9gj49>.

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