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Characterizing feral swine movement across the contiguous United States using neural networks and genetic data

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Abstract

Globalization has led to the frequent movement of species out of their native habitat. Some of these species become highly invasive and capable of profoundly altering invaded ecosystems. Feral swine (*Sus scrofa × domesticus*) are recognized as being among the most destructive invasive species, with populations established on all continents except Antarctica. Within the United States (US), feral swine are responsible for extensive crop damage, the destruction of native ecosystems, and the spread of disease. Purposeful human-mediated movement of feral swine has contributed to their rapid range expansion over the past 30 years. Patterns of deliberate introduction of feral swine have not been well described as populations may be established or augmented through small, undocumented releases. By leveraging an extensive genomic database of 18,789 samples genotyped at 35,141 single nucleotide polymorphisms (SNPs), we used deep neural networks to identify translocated feral swine across the contiguous US. We classified 20% (3364/16,774) of sampled animals as having been translocated and described general patterns of translocation using measures of centrality in a network analysis. These findings unveil extensive movement of feral swine well beyond their dispersal capabilities, including individuals with predicted origins >1000 km away from their sampling locations. Our study provides insight into the patterns of human-mediated movement of feral swine across the US and from Canada to the northern areas of the US. Further, our study validates the use of neural networks for studying the spread of invasive species.

KEYWORDS
feral pig, invasive species, neural networks, SNP, *Sus scrofa*, translocations, wild pig

1 | INTRODUCTION

With an increase in globalization, characterized by expanding human population and connectivity, species are now spreading beyond their natural dispersal capabilities to new areas (Crowl et al., 2008). Some of these species are spread accidentally, like aquatic invasive species spread by recreational boaters and commercial shipping (Haight et al., 2021), whereas others are introduced intentionally, such as domestic goats (*Capra hircus*) brought by sailors as a source of food (Campbell & Donlan, 2005; Xu et al., 2014). Although many potentially invasive species die during transit or soon after being introduced to a new area (Lodge, 1993), some will survive and propagate. These

species are referred to as invasive alien species (IAS) and can cause extensive damage to ecosystems, reduce native biodiversity, and introduce novel diseases (Horvitz et al., 2017; Ladin et al., 2023; McCreless et al., 2016). For example, invasive predators such as rats (*Rattus* spp.), mice (*Mus musculus*), domestic dogs (*Canis lupus familiaris*), feral cats (*Felis cattus*), and feral swine (*Sus scrofa* × *domesticus*; synonymous with wild pig, feral hog, and feral pig) have nearly worldwide invaded ranges, destructive behaviour, and generalist diets that make them highly successful and damaging IAS (Capizzi et al., 2014; Doherty et al., 2016, 2017; Fulgione & Buglione, 2022; Medina et al., 2011). Understanding the natural and human-mediated movement patterns of these destructive species can facilitate efforts to mitigate their spread as well as aid eradication efforts (Lodge et al., 2006; Simberloff, 2003).

Molecular methods have been successfully used to track the invasion history of IAS (Cristescu, 2015; Matheson & McGaughran, 2022). For example, the global routes of brown rat (*Rattus norvegicus*) expansion were characterized using molecular population assignment and divergence methods (Puckett et al., 2016). These assignment methods can either assign or exclude reference populations as the origin of a focal individual by using allele frequencies of the given reference populations (Cornuet et al., 1999; Latch et al., 2006; Manel et al., 2005; Piry et al., 2004). However, many species exhibit a pattern of isolation-by-distance (IBD) where individuals closer in geographic space tend to be more related. Patterns of IBD reflect spatially continuous populations rather than clear, distinct populations. Underlying patterns of IBD can result in misleading inference of population structure (Perez et al., 2018) and make assignment of individuals into their respective source populations difficult as populations are not well defined. Further, as sequencing costs have decreased over time (Goodwin et al., 2016), studies are increasingly leveraging large genetic datasets that can be computationally challenging with traditional population assignment and migrant detection methods (i.e., GENECLASS2 (Cornuet et al., 1999), STRUCTURE (Pritchard et al., 2000)). Due to these challenges, machine learning methods have been adopted as a computationally efficient alternative for population genetic analyses (Borowiec et al., 2022; Huang et al., 2023; Korfmann et al., 2023; North et al., 2021). For example, deep neural networks (a form of machine learning) have been used for genetic analysis to identify the geographic origins of modern domestic horses (Librado et al., 2021). Machine learning approaches can make predictions using general-purpose algorithms that capture patterns present in large datasets (Bzdok et al., 2018; Korfmann et al., 2023) and have shown promise in assigning individuals to their respective geographic origins using genetic data alone (Battey et al., 2020). However, this method has not been extensively used to elucidate the movement of IAS.

Feral swine are an IAS native to Europe and Asia. In the United States, feral swine have a complex introduction history descending from historical livestock husbandry practices combined with more recent wild boar introductions from native populations in Europe. Domestic swine (*Sus domesticus*) were first brought to the contiguous US (hereafter referred to as just the US) by Spanish explorers in the 1500s (Mayer & Brisbin Jr., 1991; Zadik, 2005). Subsequently, through free-range livestock management practices and ineffective

enclosures used during a period of European colonization and settlement, self-sustaining feral swine populations became established (Mayer & Brisbin Jr., 1991). In the early 1900s, wild boars were introduced from Europe for hunting and consequently hybridized with feral swine (Mayer & Brisbin Jr., 1991). As a result, a large proportion of contemporary feral swine populations (~97%) in the US are of hybrid origin, representing a hybrid swarm of feral domestic pigs and wild boar (Mayer & Brisbin Jr., 1991; Smyser et al., 2020, 2024).

In the US, feral swine cause extensive destruction, including damage to crops, property, native species, and ecosystems (Bevins et al., 2014; McKee et al., 2020; Tian et al., 2023). Native species such as ground-nesting birds (Rollins & Carroll, 2001; Sanders et al., 2020), amphibians (Canright et al., 2023), and sea turtles (Engeman et al., 2019) are imperilled by feral swine predation as well as their rooting and wallowing behaviour (McDonough et al., 2022). Further, feral swine can serve as reservoirs for numerous diseases and parasites (Baroch et al., 2015; Cleveland et al., 2024; Miller et al., 2017) including bovine tuberculosis, brucellosis (Meng et al., 2009), *Trichinella* spp. (Hill et al., 2014), and pseudorabies (Christy Wyckoff et al., 2009). Feral swine could also facilitate the spread of emerging foreign animal diseases such as African swine fever or foot-and-mouth disease (Brown et al., 2020, 2024; Meng et al., 2009). The risk of disease spillover from feral swine into livestock as well their extensive damage to crops makes feral swine management a priority for protecting food security in the US. Efforts to control and remove feral swine populations generally include exclusionary fencing, trapping, ground-shooting, aerial-shooting, and telemetered swine (Kilgo et al., 2023; Lavelle et al., 2011; McCann & Garcelon, 2008; Schuyler et al., 2002). These efforts have had varied degrees of success (McCann & Garcelon, 2008; Parkes et al., 2010). However, it is extremely difficult to eradicate established populations of feral swine due to their highly invasive characteristics. These characteristics include being an extreme generalist in habitat and diet (Barrios-Garcia & Ballari, 2012; Fulgione & Buglione, 2022), having high fecundity (5.43 foetuses/litter and multiple litters/year; Chinn et al., 2022; Snow et al., 2020), and their hybrid origins (Barmentlo et al., 2024; Fulgione et al., 2016; Smyser et al., 2020, 2024).

Despite being one of the most destructive IAS globally (Lowe et al., 2000), contemporary patterns of feral swine movement across the US are not well described. In North America, they are broadly spread across Canada, creating important threats of invasion to the northern border of the US (Aschim & Brook, 2019; Kramer et al., 2024; MacDonald & Brook, 2023). Despite having a fairly limited dispersal range (ranging from 0.5 to 2.4 km; Casas-Díaz et al., 2013), feral swine have spread to over 30 states across the US—a significant increase since the 1980s (Lewis et al., 2019). This rapid range expansion is due, in large part, to the intentional translocation of feral swine (Hernández et al., 2018; Smyser et al., 2020; Tabak et al., 2017). Further, states have differing legislation, monitoring, and enforcement regarding the movement of feral swine—which may be reflected in cross-state movement patterns. For example, state policy in Texas accommodates certain feral swine-related activities including the recreational hunting of feral swine year-round and allowing for fenced hunting preserves (4 Tex. Admin. Code § 55.9). Texas has the largest number of feral swine

in the US with a deeply seeded culture in feral swine hunting (Carlisle et al., 2022; Connally et al., 2021; Lewis et al., 2019). This hunting culture likely contributes to the growing population of feral swine through the illicit transport of feral swine to augment or introduce populations for recreational hunting (Grady et al., 2019). Conversely, Missouri has adopted a goal of eradicating feral swine from the state and has passed legislation, including the closure of public lands to feral swine hunting, as a means of eliminating the value of established populations within the state (Missouri Feral Hog Report, 2021). New policies and comprehensive control efforts have resulted in a 48.5% decrease in the number of feral swine-occupied water sheds in Missouri from 2016 to 2021 (Missouri Feral Hog Report, 2021).

Feral swine exhibit varying degrees of population structure across the US (McCann et al., 2018). Some populations are characterized by isolated groups of individuals that are relatively genetically similar while others exhibit a pattern of IBD. For example, populations in both Florida and California have been characterized by discrete, localized clusters (Hernández et al., 2018; Tabak et al., 2017). However, feral swine populations in Texas reflect a mix of spatially dispersed and weakly resolved clusters that are better described by IBD (Delgado-Acevedo et al., 2021; Mangan et al., 2021). To date, no study has evaluated widespread patterns of feral swine movement across the US. Characterizing movement patterns across the invaded range of IAS can inform management in order to improve efforts to mitigate the spread and facilitate elimination of established populations (le Roux & Wieczorek, 2009). Further, characterizing movements can help differentiate the processes of natural dispersal from those that are the result of intentional human-mediated translocation. Thus, management agencies can decide if they should focus their resources on animal movement mitigation or legislation and enforcement of human activities.

The aim of this study was to characterize the widespread patterns of movement of an IAS using machine learning and network analyses. Specifically, we characterized patterns of feral swine movement across the invaded range within the US, enabling differentiation of natural range expansion from human-mediated movement that has contributed to the expansion of this destructive species. Our objectives were to leverage a large, genomic database of feral swine to (1) characterize patterns of population structure across the invaded range within the US, (2) identify translocated feral swine using deep neural networks—focusing on translocations from within the US as well as from Canada to the US, and (3) characterize broad, spatial patterns of translocation using network analyses and a genetic distance-based neighbour-joining tree. In turn, these results can be used for developing management approaches that are tailored to the specific challenges posed by invasive species.

2 | METHODS

2.1 | Feral swine sample collection and genotyping

Biological samples ($n=18,789$) were collected from feral swine throughout their invaded range within the US as an extension of

damage management and disease surveillance efforts led by the USDA along with cooperative agencies. Overwhelmingly, samples were collected by USDA-Animal and Plant Health Inspection Service-Wildlife Services personnel. Feral swine were lethally removed through trapping or targeted sharpshooting from 2001 to 2022 as an extension of control efforts to reduce threats to agriculture, natural resources, property, and the health of humans and livestock. To identify potential translocations from Canada to the US, biological samples were collected from feral swine in Alberta ($n=13$) and Saskatchewan ($n=14$), Canada by the University of Saskatchewan under Animal Use Protocol Number 21050024. DNA extraction was performed by GeneSeek (Neogen Corporation [Lincoln, Nebraska, USA]) using various biological sample types (hair, pinna, and kidney) and the MagMax™ DNA Multi-Sample Ultra Kit (Thermo Fisher Scientific Inc. [Walthan, MA, USA]). Genetic samples were genotyped using GeneSeek's Genomic Profiler (GGP) for Porcine 80k array (68,516 loci; Illumina BeadChip microarray [San Diego, CA] licensed exclusively to GeneSeek, a Neogen Corporation, [Lincoln, NE]) and aligned to the Sscrofa 11.1 genome assembly (Warr et al., 2020).

As part of our quality control process, we removed individuals presumed to be escaped or released domestic pigs from production farms or the pet trade (i.e., Vietnamese potbellied pigs). To distinguish domestic pigs from genetically typical feral swine, we estimated the ancestry profiles of individuals based on the methods described in Smyser et al. (2020) and removed any individual with a combined ancestry of >0.4 from domestic pig breeds (Berkshire, Hampshire, Chester White, Duroc, Landrace, Yorkshire/Large White, Meishan, and miniature Siberian). Once individuals presumed to be escaped or released domestic pigs were removed, we conducted standard genotype quality control filters using PLINK 2.0 (Chang et al., 2015). First, we removed loci that were unmapped or non-autosomal based on the Sscrofa11.1 reference genome assembly (Warr et al., 2020). We then removed loci with call rates <0.95 or minor allele frequencies <0.05. Individuals were removed for downstream analyses if they were missing >5% of their genotype data. The resulting set of individual genotypes was considered the 'master' dataset. The master dataset was further pruned to create the 'training' dataset by removing related individuals as well as individuals sampled in close proximity to one another (described in the Section 2.3).

2.2 | Population structure

We used two approaches to characterize population genetic structure across the invaded range of feral swine in the US. First, we used the 'snmf' function in the R package LEA (Frichot & François, 2015) to independently characterize population structure for each state. We delineated genetic clusters within each state as states represent the spatial extent to which management actions are conducted and policy decisions are made. Further, state-level analyses allow us to capture more fine-scale patterns of population structure compared to a national-level analysis (Oyler-McCance et al., 2022). We chose the optimal number of genetic clusters (K) per state using the

cross-entropy criterion—where a smaller cross-entropy value or a plateau of values across values of K indicates the best supported K (Frichot & François, 2015). Second, we used principal component analysis (PCA) to visualize patterns of genetic structure. Specifically, single nucleotide polymorphism (SNP) genotypes were imported into R (R Core Team, 2023) using the 'read. PLINK' function in the R package adegenet (Jombart, 2008; Jombart & Ahmed, 2011), and a PCA was conducted using the 'dudi.pca' function in the R package ade4 (Dray & Dufour, 2007). To avoid bias in the PCA caused by the presence of related individuals and high variance in sample size (McVean, 2009; Novembre & Stephens, 2008; O'Connell et al., 2019), we conducted this analysis using only the individuals included in the training data (see below).

2.3 | Identifying translocations

2.3.1 | Training data

We used a deep neural network, implemented in the software Locator (Battey et al., 2020), to identify feral swine translocations. The deep neural network was trained on a set of geo-referenced individuals (the training dataset). This trained model was then used to make predictions regarding the geographic origins of individuals based solely on their genotypes. However, it is important to remove bias from this training data to get accurate predictions. To create the training dataset, we first removed highly related individuals from the master dataset to (1) ensure that familial groups would not skew allele frequencies for a given geographic region and (2) ensure that if a translocation has occurred, it is more likely that a higher frequency of individuals from the source population remains compared to the recipient location of the translocation. Similar to our genetic clustering analysis using LEA, estimates of relatedness were independently calculated for each state to best capture fine-scale patterns of population structure. To estimate relatedness (r), we used the 'pcair' and 'pcrelate' functions in the R package GENESIS (Gogarten et al., 2019). These functions implement a PCA-based method that corrects for population structure that may be present within the dataset (Conomos et al., 2016). We identified the number of principal components to retain using the 'nCng' function in the R package nFactors (Raiche & Magin, 2022). The individual with the greatest number of relatives was selected and all other individuals with a relatedness coefficient ≥0.177 (reflective of second- or first-degree relatives; Manichaikul et al., 2010) to this focal individual were removed. Second, we reduced the spatial bias in the training dataset as densely sampled areas can result in Locator functioning more like an assignment test in which samples are categorized according to their source population rather than their geographic origin (Battey et al., 2020). We removed individuals that were within 5 km of each other using the function 'thin' from the R package spThin (Aiello-Lammens et al., 2015). This process was implemented with 20 repetitions of the randomization algorithm. Most of the feral swine samples had precise geographic coordinates; however, some
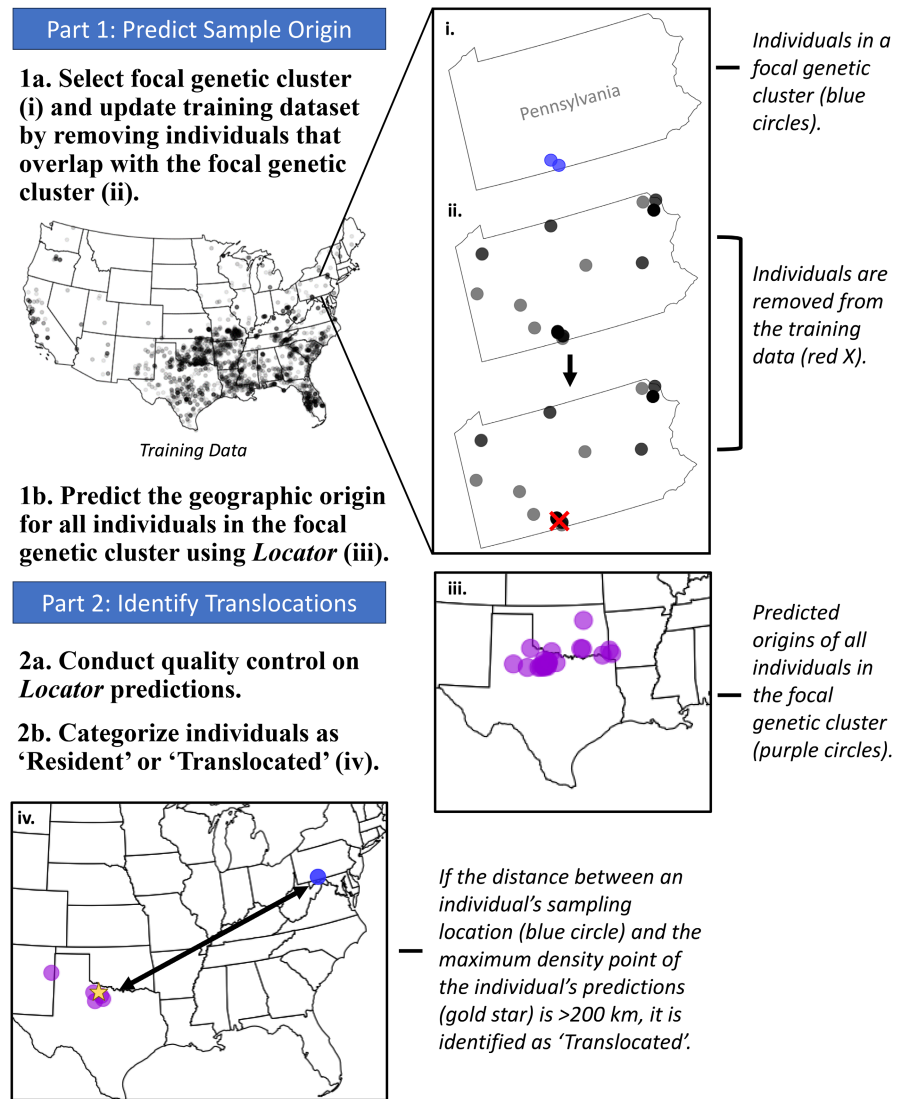
sample coordinates reflected nearby landmarks or county centroids rather than the specific sampling location. This resulted in multiple samples having the same geographic coordinates when in reality they were sampled from different localities. To accommodate this sampling artifact, we introduced variation to the geographic coordinates using the base R function jitter (factor of 65) prior to spatially thinning the dataset (R Core Team, 2023). This resulted in an average distance of 10.1 km between the sampling location and jittered coordinates (SD = 3.9 km). Lastly, we incorporated 27 unrelated individuals from Canada into the training dataset (13 from Alberta and 14 from Saskatchewan). Including individuals from Canada allowed us to evaluate origins of feral swine outside of the US. However, we lacked fine-scale spatial data for Canadian samples and, therefore, used the centroid of the respective provinces as sampling locations.

2.3.2 | Workflow

To identify translocations, we first assigned all feral swine in the master dataset to unique genetic clusters based on their admixture proportions from the LEA analysis. We then iteratively predicted the geographic origin of all feral swine by running each genetic cluster independently. To do so, we created an iterative workflow to implement Locator that encompasses the following steps (Figure 1):

1. Select a genetic cluster (i.e., a focal cluster) to use as the test dataset for Locator and remove all individuals represented in this genetic cluster from the training data. Given that Locator generates predictions based on the genotypes of the training data, predicted origins would likely resemble the sampling location if individuals from the same genetic cluster were present in the training data, even when they are the result of a translocation event.

2. Predict the origin of each individual in the focal cluster 5 times. This is done by using a different subset of individuals from the training dataset to train and validate 5 separate neural networks (90% of the training data is used for training the neural network while 10% of the training data is set aside for model validation).

3. Remove individuals that yielded high variance among the predictions from the 5 Locator iterations.
   a. Estimate the point with the maximum density of predicted locations using the 'kde2d' function from the R package MASS (Venables & Ripley, 2002).
   b. Calculate the distance between each prediction and the maximum density point.
   c. Remove all individuals where ≥3 of the 5 predictions were located more than 200 km from the maximum density point. High variance between predictions could indicate a high degree of admixture from geographically disparate populations or recent translocation to multiple areas from the same source population. In either of these circumstances, high variance between predictions indicates a low confidence in the individual's predicted origin.

FIGURE 1 Translocations were identified by using deep neural networks to predict the geographic origin for all feral swine (*Sus scrofa*) in the master dataset. The neural networks were trained using a subset of the master dataset that underwent additional filtering criteria (training dataset). Predictions were generated by independently running each genetic cluster through the iterative workflow.

Part 1: Predict Sample Origin

1a. Select focal genetic cluster (i) and update training dataset by removing individuals that overlap with the focal genetic cluster (ii).

Training Data

1b. Predict the geographic origin for all individuals in the focal genetic cluster using *Locator* (iii).

Part 2: Identify Translocations

2a. Conduct quality control on *Locator* predictions.

2b. Categorize individuals as 'Resident' or 'Translocated' (iv).

Individuals in a focal genetic cluster (blue circles).

Individuals are removed from the training data (red X).

Predicted origins of all individuals in the focal genetic cluster (purple circles).

If the distance between an individual's sampling location (blue circle) and the maximum density point of the individual's predictions (gold star) is >200 km, it is identified as 'Translocated'.

4. Categorize remaining individuals as either 'resident' or 'translocated'.
   a. Resident individuals were defined as those that had a predicted location (using the coordinates from the maximum density point) within 200 km of the respective sampling location or had a maximum density point located in the same state as the sampling location.
   b. Translocated individuals were those that had a predicted location (using the coordinates from the maximum density point) >200 km of the sampling location and had a maximum density point found in a different state than the sampling location.
5. Repeat steps 1–4 for all genetic clusters.

We ran an additional analysis to highlight in-state translocations by redefining resident individuals as those that had a predicted location within 200 km of their respective sampling location and translocated individuals as those that had a predicted location >200 km away from their sampling location. This separate analysis allowed us to identify wide-ranging feral swine movement within a given

state as well as those that originated out-of-state (Supplementary Methods in Appendix S1).

2.4 | Translocation networks

Individuals classified as translocated were used to build a network with the 'graph_from_data_frame' function in the R package igraph (Csardi & Nepusz, 2006). Nodes in the network represented states and the lines connecting nodes (referred to as edges) represented a translocation between the states. To characterize general patterns of translocations across states, we calculated several measures of centrality within the R package igraph (Csardi & Nepusz, 2006). Measures of centrality included degree, which sums all connections between the nodes. Since feral swine movement is directional (i.e., feral swine are moving from one state to another), we also changed the 'mode' argument for the 'degree' function in igraph to include all incoming and outgoing connections (the sum of all connections adjacent to the focal node), incoming connections only, and outgoing connections only. This allowed us to characterize which states

received translocations from the greatest number of states (more incoming connections) and which states were the source of translocations to the greatest number of states (more outgoing connections). To gauge the influence of a state within the translocation network, we calculated the eigenvector centrality. With this metric, states with a higher eigenvalue centrality value were connected to other states that also have high connectivity. We calculated closeness centrality to characterize how close a state was in the network to other states. In this measure, states with higher closeness centrality were also more central in the network. We also calculated the reach of each state, which is similar to the degree centrality measure; however, instead of calculating connections with adjacent nodes, the reach metric can calculate k steps out. For our translocation network, we used a normalized reach calculation with $k = 2$ (i.e., calculated to two connections out from the focal node). This was executed using the igraph function 'ego_size' and 'vcount' as (ego_size(network,k)-1)/(vcount(network)-1). The numerator of the equation, ego_size(network,k)-1, calculated the number of nodes that were included in a network composed of 2 nodes of separation from the focal node. We then subtracted 1, to remove the focal node from this count. The second part of the equation 'vcount(network)-1' calculated the total size of the full network (i.e., the number of vertices in the network) minus the focal node. By dividing the reach of a focal node, a state in this case, by the total number of nodes in the entire network, we normalized the reach score. Lastly, we calculated the betweenness centrality. This metric measured the extent that a focal node falls on the shortest path between other pairs of nodes. In other words, states with a high betweenness value likely had more influence within the translocation network. To identify redundancy between the measures of centrality, we calculated the Pearson's correlation coefficient between all measures using 'cor' function in base R (R Core Team, 2023). To identify whether state size or the number of bordering states a given state has can explain patterns of centrality, we created a series of linear models using the base R function 'lm' (R Core Team, 2023).

2.5 | Genetic distance and neighbour-joining tree

We expected translocation patterns to be complex, reflecting a process by which some states serve as a source to multiple other states. In such cases, we expected genetic similarity between all locations that receive translocations from the same source. This genetic similarity could make it difficult for the neural network to predict the origin of translocations. To elucidate the complex patterns of translocation produced by the neural network, we generated a neighbour-joining tree using the genetic distance between all genetic clusters identified in our LEA genetic clustering analysis. European wild boars were included as an outgroup ($n = 17$; Yang et al., 2017). We estimated pairwise genetic distance between genetic clusters using the 'gl.dist.pop' function in the R package dartR (Gruber et al., 2018). We generated the neighbour-joining tree using the 'aboot' function in the R package poppr using Nei's Genetic Distance between

populations with 1000 bootstrap replicates across loci (Kamvar et al., 2014; Nei, 1972).

3 | RESULTS

3.1 | Feral swine sample collection and genotyping

A total of 541 feral swine were removed prior to analyses due to either being domestic swine ($n = 515$) or having a low genotype call rate ($n = 26$). After quality control filters for individuals and loci were conducted, a total of 18,248 individuals with 35,141 loci were included in the master dataset. These samples were spatially distributed across both the established range of feral swine in the US and newly invaded area (Figure 2). After additional filtering to remove highly related individuals and reduce spatial bias, the training dataset was composed of 4100 feral swine across 38 states ($n = 4073$) and two provinces in Canada ($n = 27$).

3.2 | Population structure

State-based genetic clustering, executed in LEA, allowed us to detect fine-scale patterns of population structure. We identified some genetic clusters with strong genetic associations (genetic cohesiveness) whereas other areas were widespread and highly admixed. Using the highest proportion of cluster assignment, we categorized all feral swine into 122 unique genetic clusters across the 38 states (range = 1–10 genetic clusters/state; mean = 3.21 genetic clusters/state; Table S1). Among states with limited sampling ($n < 10$), we assigned all individuals from that state to a single genetic cluster. For our second approach using PCA, we found that the first component explained 2.451% of variation in the genetic information for all feral swine while the second explained 1.652%. We detected some wide regional differentiation, particularly differentiation of the Midwest (Illinois, Iowa, Michigan, Wisconsin, Minnesota, Indiana, Ohio, Kansas, and Missouri), the south Atlantic (Florida, Maryland, North Carolina, Virginia, Georgia, South Carolina, and West Virginia), and the south central (Arkansas, Oklahoma, Alabama, Mississippi, Louisiana, Texas, Kentucky, and Tennessee) portions of the US (Figure 3). However, genotypes from western states lacked strong association to a particular area, likely due to the fact that many western states (besides California) are newly invaded areas and may reflect introduction pressure from varying sources.

3.3 | Identifying translocations

A total of 91,240 geographic origins were predicted for all feral swine ($n = 18,248$) using Locator (5 predictions per individual). These predictions were used to identify potentially translocated individuals and identify their spatial origin. We used the known sampling location and the predicted location from Locator to estimate the
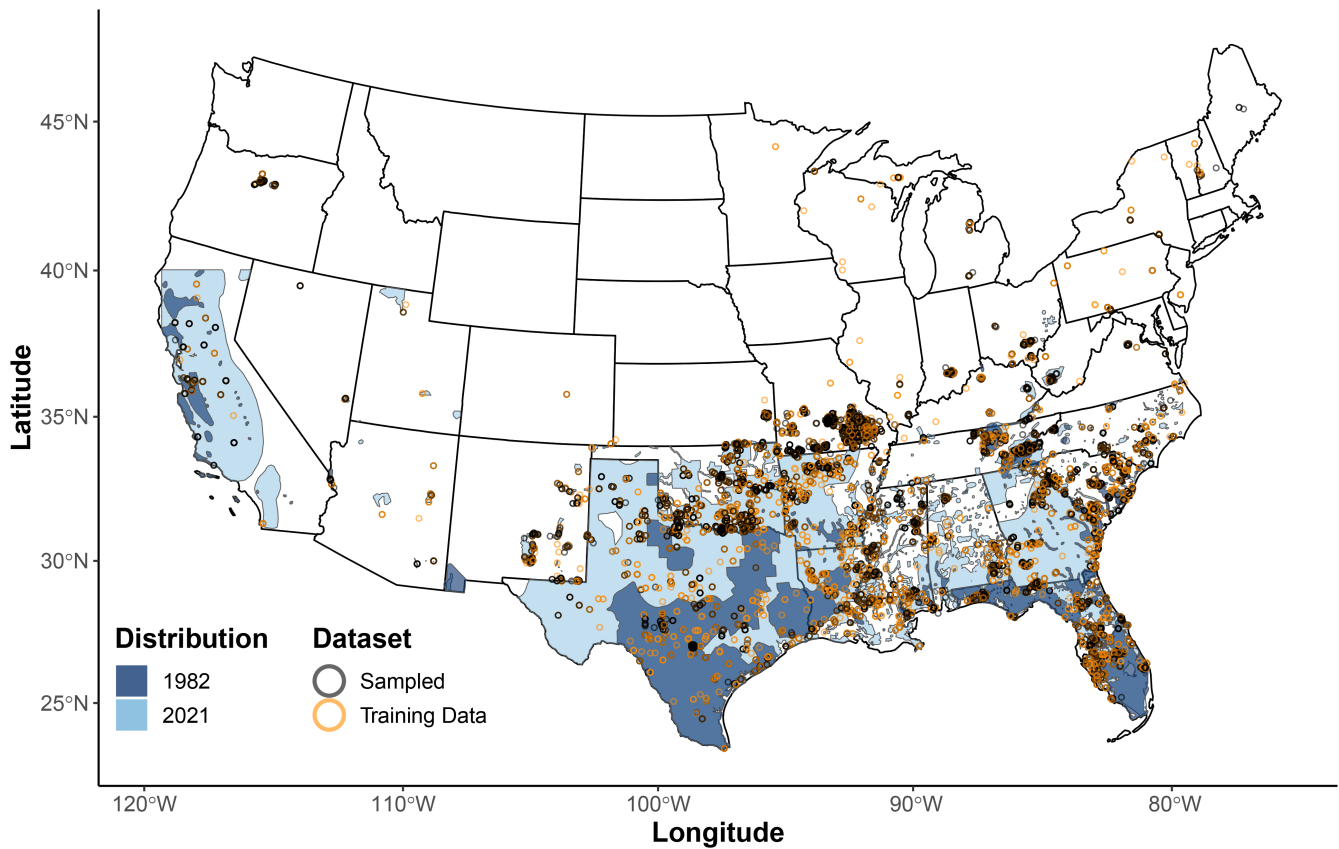
FIGURE 2 Feral swine (*Sus scrofa*) samples were collected across their invaded range in the contiguous United States. The dark blue area indicates their historic range (1982) while the light blue area indicates their contemporary range (2021). Dark grey circles represent individuals in the master data set. Orange circles represent individual feral swine that were used to train the neural network to identify translocations. Additional samples from Alberta and Saskatchewan, Canada were added to the training dataset in order to identify translocations from Canada to the United States.

prediction error of the neural network. Among individuals used for model validation, a strong correlation was observed between sampling location and predicted origin (latitude R^2 mean=.892 and range=0.757–0.969; longitude R^2 mean=.924 and range=0.798–0.983; Figure S1). Further, the prediction error was low for all iterations of Locator with a median validation error ranging from 0.130 to 0.547 degrees.

A total of 1474 individuals were removed for downstream analysis due to high prediction variance across iterations (at least 3 of the 5 predictions were more than 200 km away from the maximum density point). Of the remaining 16,774 individuals, a total of 3364 individuals were identified as translocated whereas 13,410 individuals were identified as residents (Figure S2). If we account for in-state translocations, we identified 4378 individuals as translocated (1014 from in-state and 3364 from out-of-state) and 12,396 resident individuals (Figures S3 and S4). All individuals sampled from Iowa (*n*=7), Maine (*n*=3), Michigan (*n*=24), Minnesota (*n*=1), Nevada (*n*=30), New York (*n*=19), Utah (*n*=2), Washington (*n*=5), and West Virginia (*n*=134) were identified as translocated. Further, a high proportion of individuals sampled from Arizona (71.4%), Illinois (95.5%), Kentucky (77.4%), New Mexico (77.6%), Pennsylvania (81.5%), and Virginia (88.4%) were classified as translocated (Figure S2). To

visualize broad trends of where translocated individuals originated, we plotted the maximum density point for all predicted origins at two different distance classes (Figure 4). When investigating the distribution of all predicted origins, the majority of translocations originated from coastal Georgia, Florida, the border between Oklahoma and Texas, and south-central Texas. A similar pattern was observed when evaluating only translocations originating less than 1000 km from their sampling location indicating that many translocations occur within the general region from where they were sampled. However, when we examined only translocations that originated greater than 1000 km from their sampling location, the highest density of translocations shifted from Georgia to south-central Texas (Figure 4). Further, we detected 11 long-distance translocation events from Saskatchewan and Alberta, Canada to Michigan (*n*=3), Ohio (*n*=1), and Tennessee (*n*=7).

3.4 | Translocation networks

Measures of centrality were calculated for all states. Closeness centrality for Colorado, Maine, Minnesota, Utah, and Washington could not be calculated as they were not the predicted origin of any
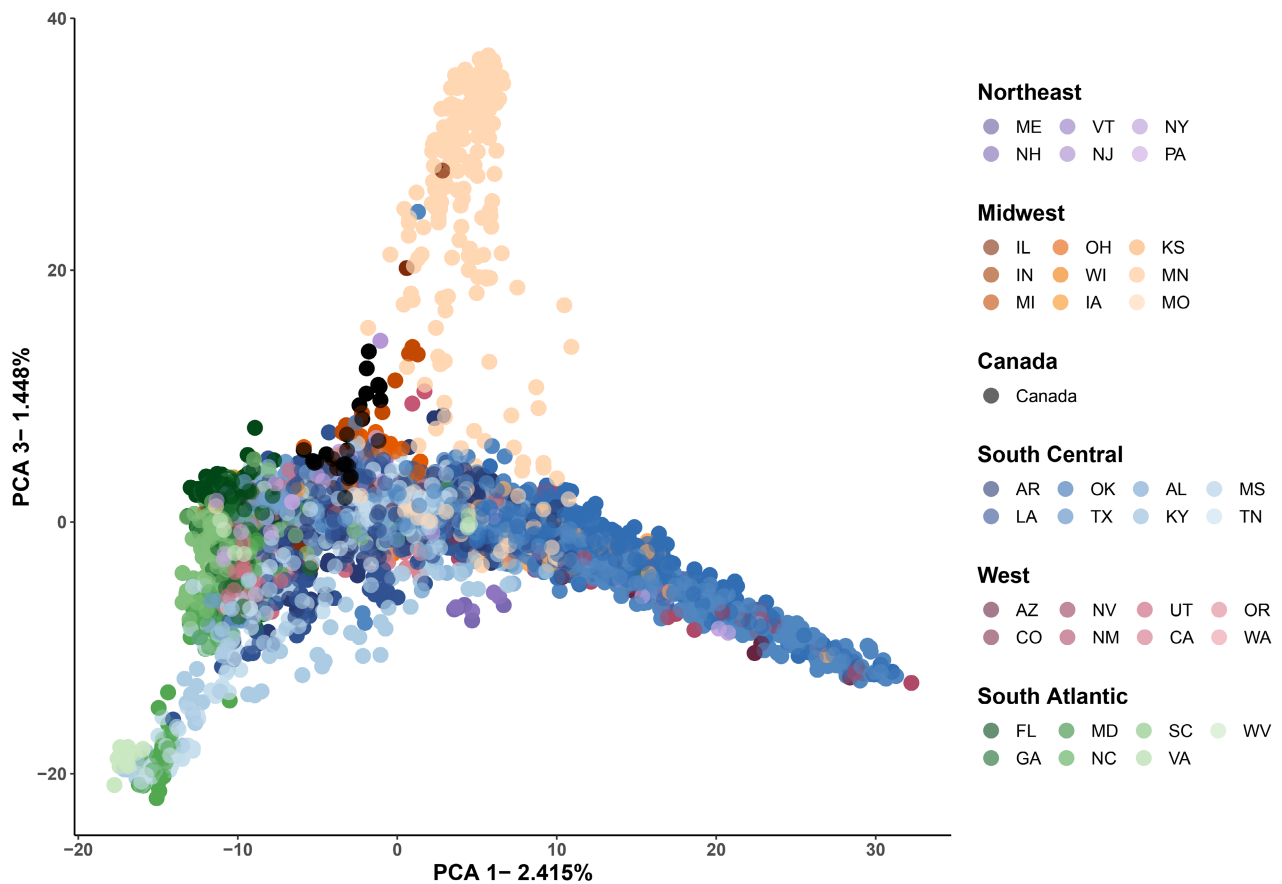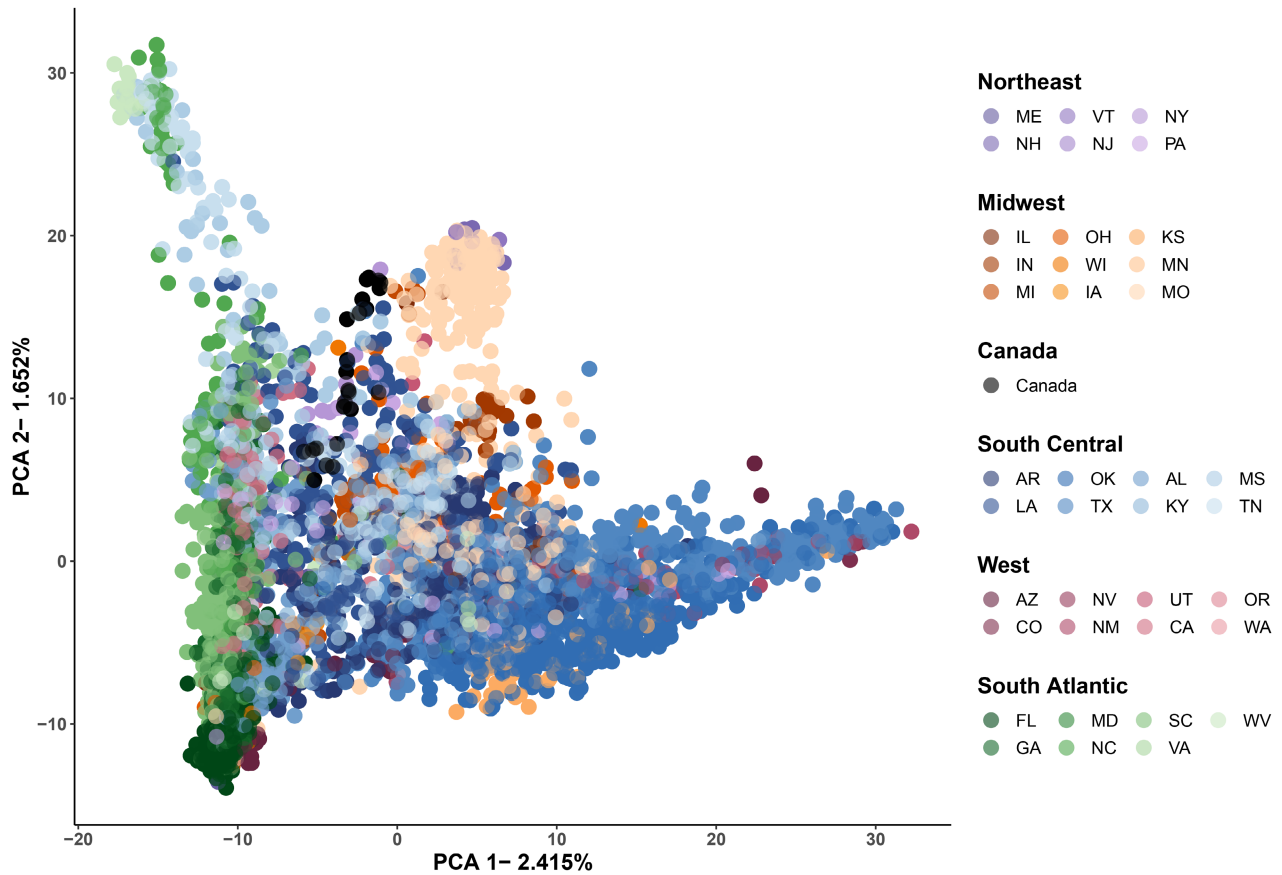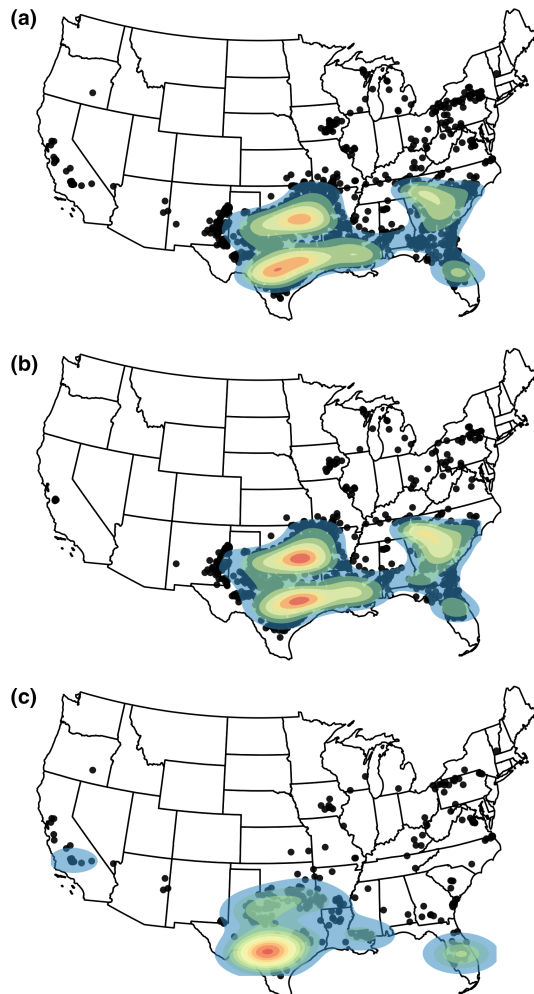
(a)

(b)

(c)

FIGURE 4 Feral swine (*Sus scrofa*) translocations were identified across the invaded range in the contiguous United States. Each point represents the predicted origin of a translocation event. Warmer colours represent a higher density of translocations relative to cooler colours. Similar patterns of translocation were observed when considering all translocation events (a) and regional translocations (those that are ≤1000 km from their sampling locations; b) while we identified Texas and Georgia as dominant sources of long-distance translocations (those that are >1000 km from their sampling locations; c).

translocations. To allow for the comparison of all centrality metrics, these states were removed prior to calculating the correlation between centrality metrics. We found two groups of highly correlated measures of centrality (cor > .8). The first group was composed of four measures of centrality: (1) the degree of incoming connections (degree in), (2) eigenvalue, (3) degree of all directions (total degree), and (4) normalized reach (Figure S5). The second group was composed of total degree, normalized reach, betweenness, degree out (only outgoing connections), and closeness. Due to this high

correlation, only betweenness, degree out (only outgoing connections), and degree in (only incoming connections) will be reported as these were among the lowest correlated and relevant for characterizing patterns of translocation.

Broadly, translocation networks revealed a higher degree of movement from the established range of feral swine in the south-central and south Atlantic regions of the US (Figure 5a). The majority of connections reflected regional translocation of feral swine (≤1000 km; Figure 5b). Texas was identified as a major source for translocations in terms of betweenness (269) and the number of outgoing connections (degree out = 93). These values were markedly higher than the other states identified as common sources of translocation (betweenness = Tennessee (93), Georgia (87) and Florida (86); degree out = Florida (17 connections), Oklahoma (14), Arkansas (14), Georgia (12), and Louisiana (12 connections); Figure 5). Tennessee was identified as a hotspot for receiving translocations based on measures of betweenness (93) and degree in (17). Many of the newly invaded states were the result of long-distance translocation (>1000 km; Figure 5c). New Mexico, Arizona, South Carolina, Kansas, West Virginia, Kentucky, Illinois, Nevada, Oregon, Vermont, Maine, Utah, Washington, Minnesota, and Colorado all had low betweenness (<10; Figure S6 and Table S2) and Colorado, Minnesota, Vermont, Oregon, Washington, Utah, Maine, Nevada, Arizona, New Mexico, and Iowa had low degree in centrality—indicating only 1–3 origins per state. Patterns of centrality could not be explained by either state size or the number of bordering states for a given state (Figure S7).

3.5 | Genetic distance and neighbour-joining tree

The neighbour-joining tree estimated from Nei's genetic distance (mean = 0.13; range = 0.01–0.38; Figure S8) revealed a few key patterns. As expected, we observed regional patterns of genetic similarity (Figure 6). For example, we observed close genetic relationships among the south Atlantic states of Georgia, South Carolina, Virginia, West Virginia, North Carolina, and Florida as well as states from the south-central region of the US (Mississippi, Alabama, Tennessee, Louisiana, and Kentucky; Clades D, E, and I; Figure 6). Samples from California and Nevada formed a subclade within Clade I. We observed close genetic relationships among a subset of states from the south-central, western, and Midwest regions (Texas, Oklahoma, Kansas, Arkansas, Missouri, New Mexico, Colorado, and Kansas; Clade G). Much like the translocation network, we observed long-ranging translocations in the neighbour-joining tree. Specifically, we see a close genetic relationship between populations sampled in western states (California, Washington, Nevada, Arizona, and Oregon) with populations sampled from the south Atlantic and south-central regions (Clade I). This indicates a history of translocation between the
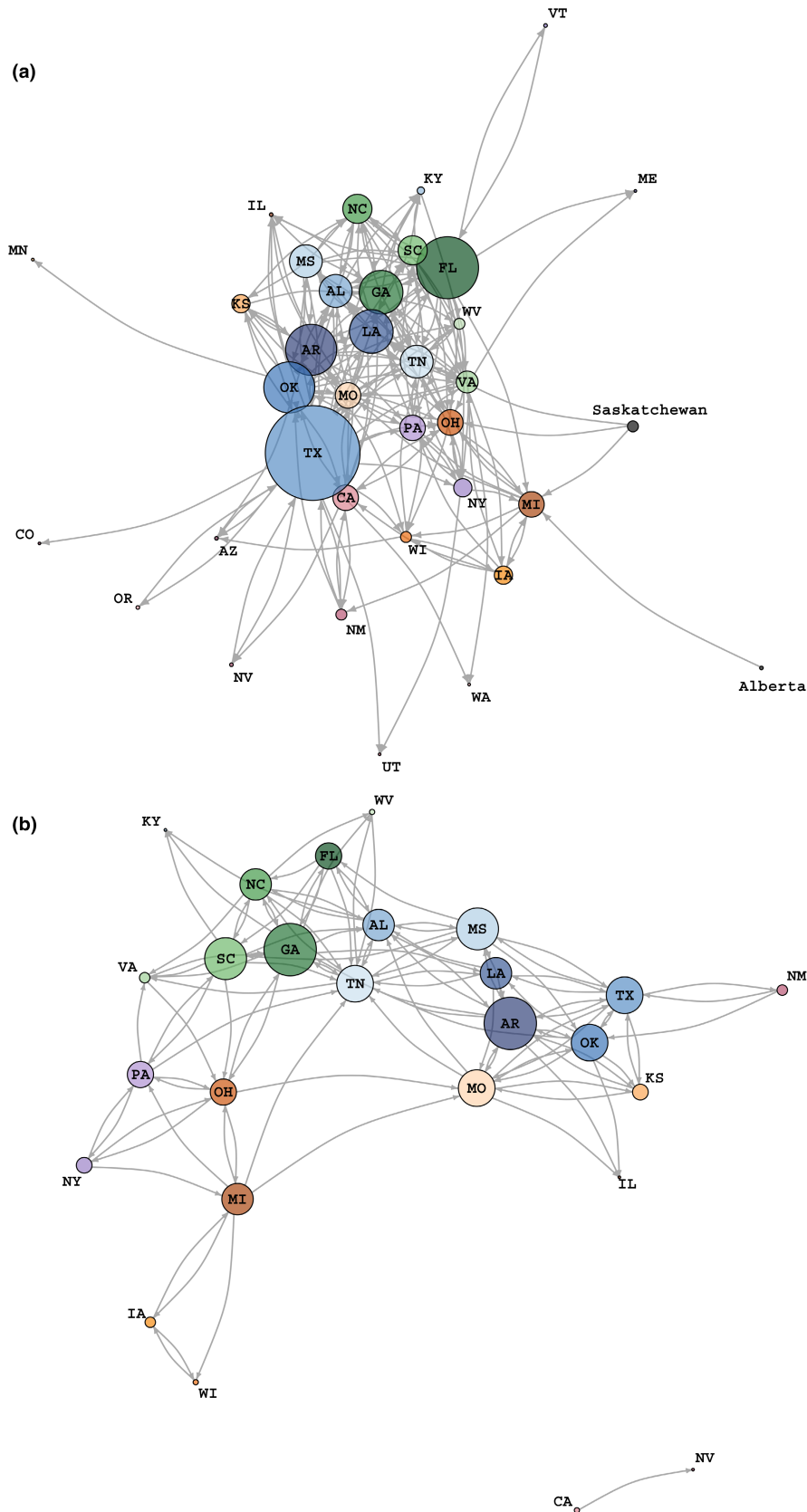
FIGURE 5 Feral swine (*Sus scrofa*) translocations were characterized between states using a directional network. Edges between nodes depict the presence of a translocation between states (nodes). The node size represents the movement of feral swine away from the focal node (degree out). Networks were generated for all translocation events (a), regional translocation events (only translocations ≤1000 km from their sampling locations; b), and long-distance translocation events (those that are >1000 km from their sampling locations; c).
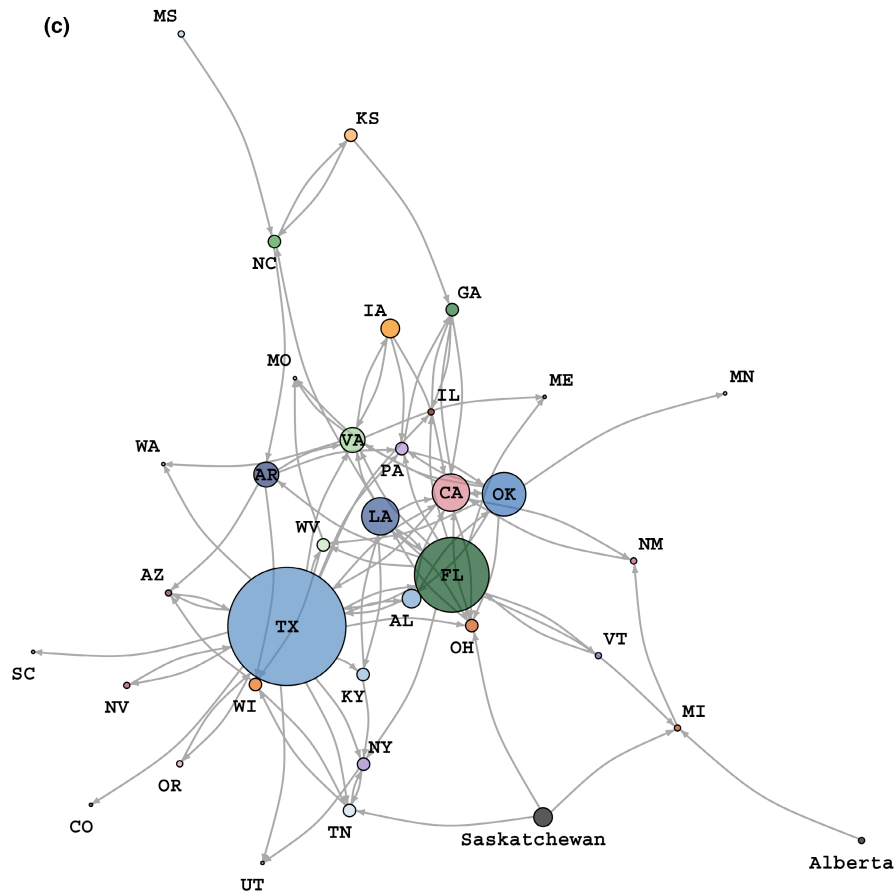
FIGURE 5   (Continued)

Pacific and Atlantic coasts. Populations from newly invaded areas of the US originated from various regions. Further, we see samples from Indiana group with samples from Alabama and Louisiana (Clade H) revealing the south-central origins of those northern populations. Samples from Illinois showed associations with California (Clade I) as well as Texas, Arkansas, and New Mexico (Clade G) indicating multiple translocations from different origins. Although geographically distant, Wisconsin showed strong associations with Oregon populations within Clade I, likely a result of translocations from the same geographic origin. A subset of populations from New York and Pennsylvania were genetically similar to those found in Oklahoma and Texas (Clade G). Populations in Northern states (Pennsylvania, Michigan, Ohio, New York, Vermont, New Jersey, New Hampshire) generally grouped together with the Canadian provinces (Alberta and Saskatchewan) and were more closely related to pure European wild boar than other feral swine populations from the US (Clades A, B, and C).

4 | DISCUSSION

Understanding the movement patterns of IAS is critical in taking steps to mitigate their spread. In this study, we leveraged genomic data and machine learning to characterize drivers of invasive species expansion. In implementing this approach, we successfully identified and characterized patterns of human-mediated feral swine translocations. As removing established populations of feral swine is difficult and does not curtail their range expansion when movement is facilitated by humans, management efforts should be focused on mitigating the introduction of feral swine into new areas. In this study, we have highlighted the potential sources of translocated individuals to newly invaded areas and have shown that translocations across state borders are widespread and frequent. With this information, management strategies can be tailored to mitigate the anthropogenic spread of feral swine. For instance, movement information can be used to inform invasive species management models (ISMMs; Thompson et al., 2021) and prioritize management efforts (Baker, 2017; Pepin et al., 2020). Legislation, enforcement, and monitoring are integral components of an effective response for states, particularly those on the front of the invaded range, to reduce human-mediated movements of feral swine and expansion of their distribution.

Broad, regional patterns of genetic structure were identified using PCA and were consistent with patterns of genetic structure described in McCann et al. (2018) (Figure 3). Similar to previous work characterizing genetic structure of feral swine in Florida (Hernández et al., 2018), California (Tabak et al., 2017), and Texas (Delgado-Acevedo et al., 2021; Mangan et al., 2021), we found
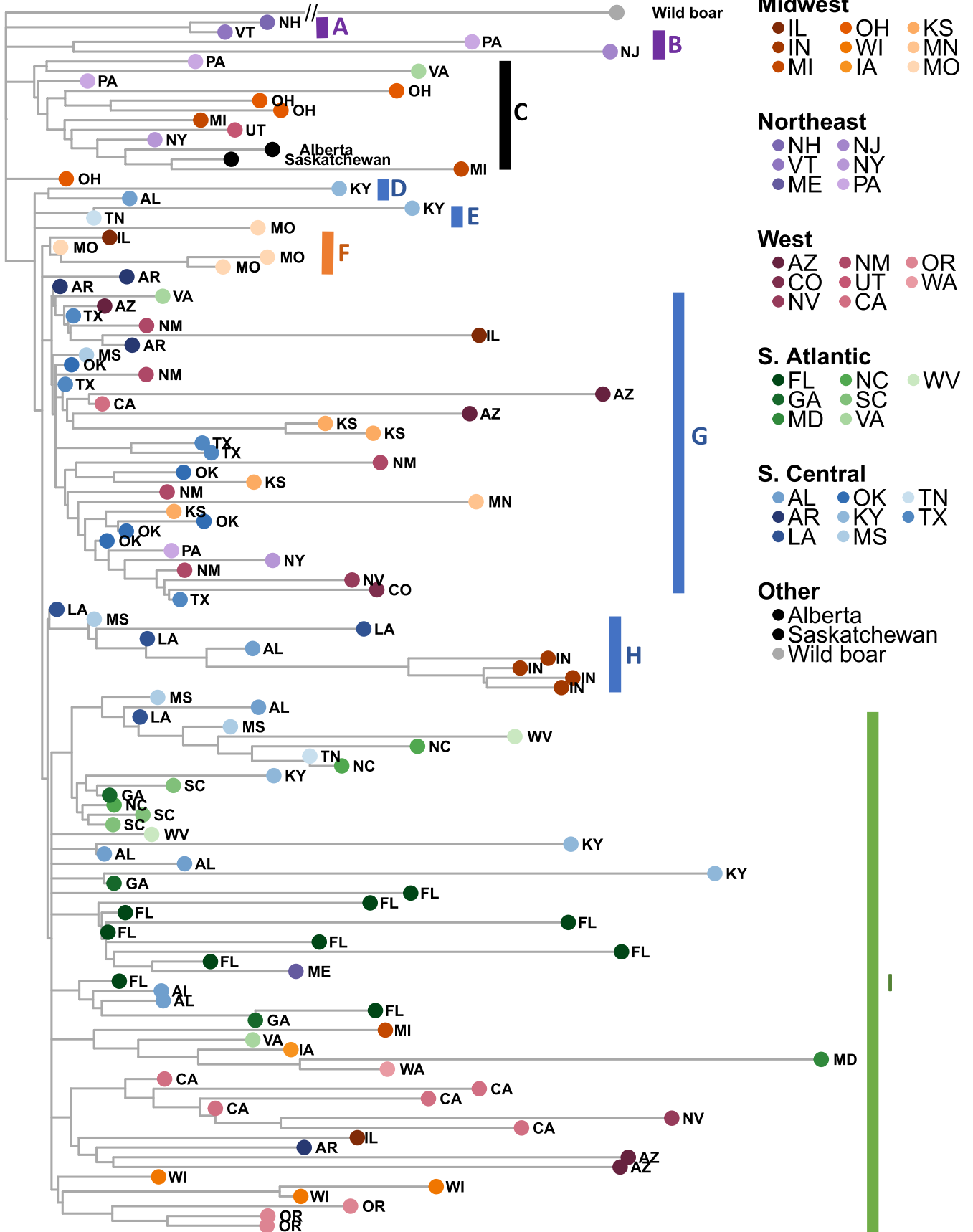
Midwest
- IL
- IN
- MI
- OH
- WI
- IA
- KS
- MN
- MO

Northeast
- NH
- VT
- ME
- NJ
- NY
- PA

West
- AZ
- CO
- NV
- NM
- UT
- CA
- OR
- WA

S. Atlantic
- FL
- GA
- MD
- NC
- SC
- VA
- WV

S. Central
- AL
- AR
- LA
- OK
- KY
- MS
- TN
- TX

Other
- Alberta
- Saskatchewan
- Wild boar

several areas across the contiguous United States that exhibited weak genetic structure (patterns of IBD) whereas other areas reflected more distinct, isolated genetic clustering. Feral swine dispersal in North America ranges from 0.5 to 2.4 km (Casas-Díaz et al., 2013); therefore, weak genetic structure could be a result of close, interconnected genetic populations with dispersal between them (stepping-stone model) or could be facilitated by translocation. Despite weak genetic structure in some regions of the US, the deep neural network created by Locator frequently predicted the origin of a sample with less than 1 degree of error from the sampling location. As predictions made by Locator are estimated to be accurate within 3.16 to 4.09 generations of dispersal (Battey et al., 2020), our validation error is slightly higher than expected but sufficient to characterize broad-scale patterns of feral swine movement. Further, estimates of dispersal for newly established populations could be higher based on the number of feral swine translocated and the habitat quality of the new area (Clontz et al., 2023).

Despite low validation error within the deep neural networks, the neural network was not without its limitations. A total of 20.7% of samples were removed from the translocation analysis due to high variability in the predicted origins for a given individual among Locator iterations. Highly variable predictions could occur for several reasons. For example, if a translocated feral swine is released into an area with an established population and breeds with a resident individual, the offspring would have genetic associations to the disparate geographic locations of both parents and result in high spatial variance among predictions. Conversely, if a specific genetic population is used as a source for translocations to multiple other regions, it may be difficult to pinpoint which region is the source using only genetic data. Specifically, Locator could assign an animal to either the original source or the opposing seeded population. Neural networks are also influenced by bias in the data used for training the network and spatial bias can lead to higher prediction error (Battey et al., 2020; Rehmann et al., 2024). We conducted 'downsampling' to reduce spatial bias present in the training data by removing related individuals as well as individuals in close proximity; however, some areas were still overrepresented in the training data (Figure S9). Although this may have impacted the predicted origin of individuals, we identified Texas as one of the biggest sources of translocation even though it had a relatively low sampling density based on the size of the state (Figure S10). Conversely, Missouri had a relatively low degree out measure of centrality (i.e., it was not a large contributor of translocations) but had a higher sampling density compared to Texas. This leads us to believe that sample bias had a limited impact on our predictions. Further, a balance between having enough samples

to properly train the model and reducing sampling bias could lead to reduced prediction error (Rehmann et al., 2024). Specifically, excessive down-sampling can reduce mean prediction bias, but increase prediction error (Rehmann et al., 2024). Despite these challenges, we were able to characterize a clear pattern of translocation across the US by pairing our translocation results with a neighbour joining tree of the genetic distance between genetic clusters. The neighbour-joining tree served as a compliment to elucidate the complicated relationships among feral swine populations with admixed origin or when populations are established from similar genetic populations.

Similar to the translocation network, the neighbour-joining tree highlighted the extent of regional movement as well as revealed patterns of long-ranging translocations (>1000 km). For instance, an Illinois population was predicted to have originated from Texas in the translocation network. The neighbour-joining tree showed associations with Texas populations and with Missouri (Clade F) suggesting these populations could have come from a common source (Figure 6). Similarly, the translocation network identified potential translocations from Canada to Michigan, Ohio, and Tennessee. The neighbour-joining tree confirmed strong associations between Michigan, Ohio, and Canada. These populations were also more genetically similar to European wild boar than to the other feral swine populations in the US. The only other documented translocation from Canada to the US was a free-ranging wild pig euthanized in New York in 2017 with a Saskatchewan ear tag that proved it originated from Saskatchewan, Canada in 2004 and escaped from a New York animal sanctuary (Michel et al., 2017). The neighbour-joining tree conflicted with the translocation network in some relationships. For example, 30 individuals from Ohio were predicted to be from California based on the translocation network, but Ohio individuals have strong association with other Midwestern states in the neighbour-joining tree. Further, the translocation network predicted the source of Oregon translocations was Texas; however, the neighbour-joining tree showed Oregon populations in Clade I more closely related to south Atlantic states and a subset of south-central states that do not include Texas. However, these populations may have ancestral sources from Texas themselves. Lastly, the neighbour-joining tree highlights the degree of relatedness among all populations in the US. This helps identify possible translocations that have been in isolation and those that have a high degree of ongoing gene flow.

Overall, we found that feral swine are being translocated across the US with many states receiving translocations from just a few states (1–3), while others receive from greater than 10 states (Tennessee, Texas, Ohio, Georgia, Alabama, Virginia, and Missouri). We found that areas in Georgia, southern Oklahoma, central Texas,

southern Louisiana, and central Florida were hotspots for the origination of translocations. However, if we focus on only long-distance translocations (greater than 1000 km from sampling location), central and northern Texas as well as Florida are the main sources of translocations (Figure 5). This pattern is also reflected in our network analysis with Texas, Louisiana, Georgia, Arkansas, Florida, and Oklahoma having the highest degree out centrality values. However, it is important to note that Texas had a notably higher value of degree out centrality compared to the next highest state and had a substantially higher measure of betweenness than any other state. This suggests that Texas serves as an important source for translocations across the United States (serving as a source to 26 of the 38 states we investigated) and has a disproportionate impact on the spread of feral swine. It is possible that the difference in state legislation pertaining to the possession and transport of feral swine, as well as local hunting culture, can explain these patterns of translocation pressure. Further studies are needed to quantify the sociological factors that influence translocation rates.

In this study, we have demonstrated how genetics and neural networks can be effectively used to characterize patterns of IAS movement. By understanding the patterns of IAS movement, we can aid and inform management efforts to improve food security and mitigate ecological destruction. We found that there is substantial human-mediated movement across the contiguous United States and have documented long-distance translocation from core invaded areas (Texas) to emergent populations (Pennsylvania and New York). Models have shown that much of the central and eastern regions of the US are vulnerable to invasion by feral swine in the future (Miller et al., 2023), and we characterized translocations as a source to many of these areas. Preventing the spread of feral swine is vital to protecting biodiversity and native species as well as controlling the spread of disease (Brown et al., 2020). Further, targeted mitigation efforts are the most impactful way to manage IAS. However, feral swine regulations and management vary among states and are influenced by social and cultural factors (Smith et al., 2023), which can challenge efforts to mitigate translocation. It is our hope that the results of this study help target limited resources available for controlling this destructive IAS towards mitigating the spread and ongoing introductions from identified core source areas.

AUTHOR CONTRIBUTIONS

Rachael M. Giglio: Designed research; performed research; analysed data; writing – original draft; writing – reviewing and editing. **Courtney F. Bowden:** Designed research; performed research; analysed data; writing – reviewing and editing. **Ryan K. Brook:** Contributed samples; writing – reviewing and editing. **Antoinette J. Piaggio:** Designed research; writing – reviewing and editing. **Timothy J. Smyser:** Designed research; writing – reviewing and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Genotype data and the associated metadata (including sampling county and state) for the invasive feral swine are available through Dryad data repository (https://doi.org/10.5061/dryad.b2rbnzsq9). Additionally, filtered wild boar genotypes used in the neighbour-joining tree (originally published in Yang et al. (2018)) are available through Dryad data repository (see below link). Yang et al. (2018). Data from: Genome-wide SNP data unveils the globalization of domesticated pigs [Dataset]. Dryad. https://doi.org/10.5061/dryad.30tk6.

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