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Anthropogenic factors predict movement of an invasive species

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Abstract. Humans are playing an increasingly large role in the expansion of invasive species' distributions, but few (if any) studies have evaluated anthropogenic factors associated with intentional translocation of invasives. The wild pig (*Sus scrofa*) is an extremely destructive and rapidly expanding invasive species whose movement is thought to be facilitated by humans. We sought to (1) identify a suite of genetic markers that can be applied to population genetic analyses of wild pigs, (2) find quantitative evidence of human-mediated dispersal of wild pigs, and (3) determine which anthropogenic factors were associated with their translocation. We identified 43 polymorphic microsatellite loci and employed population genetic analyses to evaluate population structure and movement of wild pigs among populations in California, USA. Hierarchical Bayesian models were used to evaluate the influence of anthropogenic covariates on wild pig movement, and to predict migration risk. Natural dispersal of wild pigs among populations was low, as indicated by a large number of genetic clusters ($K = 21$), significant population differentiation, and low rates of recent migration. This suggests that the observed movement resulted from human-mediated translocation. Movement of pigs was positively predicted by the number of domestic pig farms, the number of captive game hunting farms, the amount of public land, the number of wild pigs harvested by hunters, and the number of game outfitters. While hunting has been hypothesized to play a role in wild pig movement, our study is the first to provide quantitative evidence of such a relationship. We argue that future efforts to manage invasive species must consider the potential role of humans in their dispersal.

Key words: Anthropocene; anthropogenic dispersal; Bayesian hierarchical models; Bayesian model averaging; feral swine; global change; invasive alien species; invasive wild pigs; leave-one-out cross-validation; population genetics; *Sus scrofa*; translocation.

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INTRODUCTION

The geographic ranges of many invasive species are increasingly being driven by human-mediated movement (Hulme 2015, Buckley and Catford 2016). Anthropogenic movements of invasive species threaten biodiversity and agriculture, modify ecosystems, facilitate the spread

of harmful pathogens over long distances (e.g., chytridiomycosis and sudden oak death), and impede conservation efforts (Banks et al. 2015, Kuebbing and Nuñez 2015). Movement of plants and invertebrate animal species (e.g., *Ambrosia* spp. and *Dreissena polymorpha*) is often an unintentional consequence of human long-distance travel, international trade, and

globalization (Perrings et al. 2005, García-Díaz et al. 2015). Historically, the prediction of invasive species distribution and range expansion has focused on natural dispersal (Kot et al. 1996, Guisan and Thuiller 2005). Such attempts often ignore anthropogenic effects, which for some species might be the greatest driver of range expansion (Waithman et al. 1999).

In North America, many vertebrate species have been introduced and moved, often for the purposes of recreational hunting and fishing (Geist 1985, Johnson et al. 2001, Cambray 2003). There are at least 125 free-ranging exotic mammal species in North America (Belden 1994, Mungall and Sheffield 1994), many of which have been intentionally imported, moved, and released for sport hunting (Pine and Gerdes 1973, Butler et al. 2005). Despite the extensive research on exotic and invasive species, the linkage of anthropogenic mechanisms that underpin intentional human-mediated range expansion of invasive mammals remains unstudied in the ecological literature. Providing evidence and quantifying human-mediated spread of invasive species can help managers predict areas at high risk of having invasive species introduced, support mitigation strategies, encourage legislation to stop introductions, and identify populations requiring management.

The wild pig (*Sus scrofa*) is invasive to, and widely distributed across, North America (Brook and van Beest 2014, McClure et al. 2015); it causes a tremendous amount of damage to wildlife, native ecosystems, and agriculture (Cushman et al. 2004, Parkes et al. 2010) and is a vector of harmful zoonotic pathogens (Meng et al. 2009). The wide distribution of wild pigs in North America is largely a result of human stocking of populations over the last five centuries (McCann et al. 2014). Humans continue to move wild pigs, a process that facilitates their expansion and complicates management efforts (Bevins et al. 2014). Legal and illegal movement of pigs for sport hunting is thought to be a primary mechanism driving wild pig range expansion globally (Pine and Gerdes 1973, Barrett 1977, Wood and Barrett 1979, Spencer and Hampton 2005, Sweitzer et al. 2015). However, there is little quantitative evidence of human movement of wild pigs, and attempts to quantify the association between anthropogenic factors and translocation remain elusive.

We coupled state-wide population genetic analyses of wild pigs in California with hierarchical Bayesian models to quantify anthropogenic factors that are associated with human-mediated movement into, and out of, counties (or immigration and emigration, respectively). We hypothesized that wild pig emigration would be positively associated with wild pig density and the importance of the recreational hunting industry in the county. We used hunter harvest as a proxy for the availability of wild pigs for capture and translocation. To measure the importance of recreational hunting, we used the number of licensed game outfitters present in the county.

We evaluated three covariates with potential roles in wild pig introduction into counties: game farms, domestic pig farms, and public land. The game farm industry (farms where customers can hunt captive animals) has been associated with the introduction and release of exotic, and often invasive, species for the purposes of recreational hunting (Geist 1985, Demarais et al. 1990, Butler et al. 2005). Specifically, game farms are thought to be associated with the movement and release of wild pigs for hunting purposes in several regions of the United States (Mayer and Brisbin 2008). Additionally, domestic pigs are known to be a source for established feral swine populations (Brook and van Beest 2014). Domestic pig escapes are common, especially with small farms, and have been established as a source of feral swine populations (Morelle et al. 2016). It is also common for domestic heritage pigs to be purchased and released for the purpose of establishing hunting populations (Scandura et al. 2011). Finally, public land has been identified as a potential location for new wild pig populations (Hartin et al. 2007, Loggins 2007). Therefore, we hypothesized that immigration of wild pigs would be positively associated with game farms, domestic pig farms, and public land.

Here, we search for quantitative evidence that humans have moved wild pigs in California, identify anthropogenic factors associated with the movement of wild pigs, and predict the probability of wild pig immigration and emigration for each county in the state. We describe ways that an improved understanding of human-mediated movement, and the anthropogenic factors associated with translocation, can be used to

mitigate against the harmful effects of wild pigs and help curb the ongoing spread of this invasive species in North America. Future efforts to manage invasive species will require an improved understanding of the anthropogenic factors associated with translocation.

METHODS

Data acquisition

Wild pigs on mainland California were captured opportunistically in traps from control efforts and hunters between June 2005–October 2008. Locality data for individual pigs were collected at the county level. Wild pigs on Santa Cruz Island were sampled during an eradication program (Parkes et al. 2010). Domestic pigs (i.e., black, Duroc, Hampshire, white, York, and cross-breeds) were subsampled from an archive at the University of California, Davis. Blood, muscle, or hair samples were collected from each individual for genetic analyses.

Microsatellite loci were identified from the domestic pig genome (Archibald et al. 1995, Alexander et al. 1996, Rohrer et al. 1996). Initially, 85 loci were identified for testing in wild pig populations from California. After preliminary tests of amplification, polymorphism, and multiplexing, a subset of 43 loci were selected to be applied to the total set of samples (Appendix S1). Details of methods for polymerase chain reaction are available in Appendix S2.

Population genetics

MICROCHECKER v.2.2.3 (Van Oosterhout et al. 2004) was used to assess null allele frequencies across 43 loci using a Bonferroni correction with a 95% confidence interval for 10^4 iterations. The Brookfield 1 index (Brookfield 1996) was applied, and loci with <15% null alleles were retained (Dakin and Avise 2004). We used ARLEQUIN v.3.5.1.2 (Excoffier and Lischer 2010) to calculate basic diversity indices across all samples (number of alleles, N_A ; expected heterozygosity, H_E), calculate Nei's gene diversity (Nei 1987), and estimate F_{ST} among inferred genetic clusters (described below). GENEPOP v.4.5 (Raymond and Rousset 1995) was used to calculate Hardy–Weinberg equilibrium (HWE; 10^6 steps in Markov Chain and 10^5 dememorization steps) and linkage disequilibrium (LD; 10^4 permutations). Sequential

Bonferroni corrections were performed to adjust significance levels for multiple tests of F_{ST} , HWE, and LD (Holm 1979, Rice 1989).

To assess population structure, we used two Bayesian approaches to detect genetic clusters (K) within the total data set. The first approach was implemented in BAPS v.6.0 (Corander and Marttinen 2006, Corander et al. 2008a) to estimate K distributed among individuals without information about capture locality (Corander et al. 2008b). We ran BAPS initially with five replications of $K = 1$ –25 and then, based on those results, final analyses were conducted with 20 replications on the K values with the highest likelihood ($K = 15$ –22). Another approach used to estimate K was accomplished in STRUCTURE v.2.3.4 (Pritchard et al. 2000, Falush et al. 2003) as it implements a different algorithm than BAPS. STRUCTURE was run with a burn-in of 10^6 and 10^6 Markov chain Monte Carlo (MCMC) repetitions post-burn-in. The remaining parameters were set to default (admixture for ancestry and correlated allele frequencies). We tested K from 1 to 25 with 20 replications of each to assess stability between runs (Waples and Gaggiotti 2006). To determine the optimum value for K based on the STRUCTURE runs, ΔK , a statistic based on the rate of change in log-likelihood of the data (Evanno et al. 2005) was calculated using STRUCTURE HARVESTER v.0.6.94 (Earl and vonHoldt 2012). Once we identified optimal K , individuals were divided into their assigned clusters and genetic differentiation (F_{ST}) was calculated among these clusters using 10^4 permutations in ARLEQUIN.

Rates of recent migration were estimated among each of the sampling locations (i.e., counties, island zones, or domestic breeds) using a Bayesian algorithm implemented in BAYESASS v.3.0.3 (Wilson and Rannala 2003). We used this program to estimate movement among populations and movement of individual pigs within the last three generations. To identify movements among populations, 10^8 MCMC iterations were used following a burn-in period of 10^7 and a sampling interval of 500 steps. Chains were compared to a stationary posterior distribution for convergence by performing multiple runs with dispersed starting values. Proportion of individuals that were assigned as migrants (migration rates) and associated 95% credible intervals (CIs) were estimated among each of the sampling

locations. BAYESASS also provided estimates of migration for individuals (i.e., the posterior proportion of the ancestry of each individual that was from other locations). Migration rates were classified as negligible if the 95% CI overlapped zero and as significant if the CI did not include zero. Estimated rates of individual migration from BAYESASS were compared to their cluster assignment from BAPS to assess concurrence between these analyses for each individual.

Evaluating probability of wild pig migration

We modeled the effects of several covariates on migration rates among sampling locations (i.e., the mean posterior proportion of a county that was assigned as migrants by BAYESASS) to test the hypotheses of social factors contributing to human-mediated movement of wild pigs. Models were run separately using immigration and emigration as response variables, where immigration was the proportion of individuals who were migrants into a county (i.e., the sum of proportion migrants from all other sampling locations) and emigration was the proportion of individuals that migrated out of a county (i.e., the sum of proportion migrants into all other sampling locations). Predictor variables for migration in each direction included the mean number of pigs harvested by hunters in a county between 1994 and 2014 (*hunter harvest*; California Department of Fish and Wildlife 2015), the number of registered game outfitters (i.e., outfitters for all game, not just wild pigs) in a county (*game outfitters*; California Department of Fish and Wildlife 2014), the mean number of game farms across years from 2002 to 2012 (*game farms*; USDA 2015), the mean number of domestic pig farms across years from 1997 to 2012 (*pig farms*; USDA 2015), and an index of the amount of public land (in km²; *public index*). Each of the covariates was scaled and standardized prior to analyses.

Three of these covariates require more explanation. Game farms focused on Cervids make up the majority (68%) of the game farm industry in the United States (Anderson et al. 2007a, b), and the absolute number of game farms in a county was not available. Thus, we used data describing the number of Cervid game farms in the county as a measure of the game farm industry size (USDA 2015). For pig farms, the number of domestic pig farms available from the United States

Department of Agriculture's National Agricultural Statistics Service in a county was used as a measure of the availability of domestic pigs both as escapees and for purchase and release by hunters (USDA 2015). The public index was constructed to provide an estimate of the amount of public land that was suitable for wild pig introduction and sustainability. First, the amount of public urban land area (in hectares; California Department of Transportation 2015) in a county was subtracted from the total amount of public land (USGS 2015). Then, the amount of public land was weighted by the relative probability of wild pig occurrence (McClure et al. 2015) in the county.

Generalized linear models (GLMs) in a hierarchical Bayesian framework were applied using Stan v.2.9.0 (Stan Development Team 2015a), with the R package "rstan" (R Core Team 2015, Stan Development Team 2015b) to fit models for immigration and emigration. The full models included the fixed effects of five predictor variables (*hunter harvest*, *game outfitters*, *game farms*, *pig farms*, and *public index*) on migration. Reduced models considering all possible combinations of covariates were also applied. The response variable (proportion of migrants) was treated as a beta-distributed random variable. To estimate the posterior, we used the "no-u-turn sampler" algorithm (Homan and Gelman 2014), using four chains of 5000 iterations, half of which were used as warmup (after confirming that this was sufficient for model convergence). For each model, we calculated Watanabe-Akaike Information Criterion (WAIC). Bayesian model averaging was conducted to obtain posterior distributions for each parameter based on the entire suite of models (Hooten and Hobbs 2015). We used the covariate values for each county in California (including those for which we did not sample wild pigs) and the model-averaged GLM β s to predict the probability of immigration and emigration for each county. We evaluated the predictive ability of our models using leave-one-out cross-validation (Rennie et al. 2005, Hooten and Hobbs 2015). For each county, we used a training data set that included all counties except this county and ran the entire suite of models (including Bayesian model averaging) and used these estimates to predict the migration rate for the county that was left out (Gelman and Hill 2006). We then compared predicted migration rates from this

cross-validation procedure to the migration estimates from BAYESASS using Spearman's rank correlation (Boyce et al. 2002).

RESULTS

None of the 43 loci had >13% null alleles per locus so all were retained for subsequent analyses. A total of 736 individuals were genotyped to some degree. Individual genotypes that were from counties or domestic breeds with less than four individuals genotyped and genotypes that were <20% complete (fewer than 35 loci) were removed. The final data set used for these analyses included 699 individuals from 25 sampling locations (16 counties, three Santa Cruz Island zones, and six domestic breeds). Demographic data (age and sex) were not necessarily collected for each individual (the implications of the absence of such data are described below).

Across all loci, the N_A ranged from 6 to 36 (median = 9.0, mean = 11.2, standard deviation [SD] = 6.1). Genetic diversity was moderate with H_E across loci ranging from 0.03 to 0.90 (median = 0.66, mean = 0.59, SD = 0.24), and overall Nei's diversity was 0.57 ± 0.28 . At each sampling location where a locus was polymorphic, there was no significant LD among loci and there were no significant deviations from HWE.

The number of genetic clusters with the lowest log-likelihood in BAPS was $K = 21$. Clusters generally formed geographical units (Fig. 1a). Analyzing population structure using STRUCTURE and STRUCTURE HARVESTER also revealed $K = 21$. Individual membership to clusters was analogous between both algorithms. When F_{ST} was estimated among these clusters (210 total pairwise comparisons), all pairwise F_{ST} values were significantly different from zero except for 17 comparisons (Appendix S3). Of these 17 comparisons, all had $F_{ST} \geq 0.19$, and most (11) involved one cluster that was comprised of only two individuals that were both identified as migrants from Trinity County into Mariposa County by BAYESASS. Of the remaining six insignificant comparisons, F_{ST} values were high (>0.25), and five of these F_{ST} values were >0.31, indicating high genetic differentiation among clusters (Hartl and Clark 2006, Frankham et al. 2010). Therefore, combining results led to identification of 21 differentiated populations in

California that were geographically associated and had little gene flow among them.

There were negligible rates of migration among most of the sampling locations, further confirming low overall gene flow. Of 600 sampling location-level migration rates that were calculated (from each sampling location into every other sampling location), only 18 were significant (i.e., the 95% CI for proportion of individuals assigned as migrants did not overlap zero; Appendix S4). Of the migrants that were identified, the largest distance across which significant migration occurred at the level of the sampling location was 360 km; $11.4\% (\pm 5.0\%; 95\% \text{ CI})$ of the individuals in Trinity County were migrants from San Benito County. Additionally, at the level of the sampling location, some individuals in Trinity County were assigned as migrants from the black domestic breed ($7.2\% \pm 4.9\%$) and from the white domestic breed ($5.3\% \pm 4.8\%$; Appendix S4). However, this migration between domestic and wild pigs was not observed when examining the posterior assignment for individual pigs in the output from BAYESASS or BAPS.

Comparing the results of individual-level migration from BAYESASS and BAPS revealed that these two algorithms produced similar results. Individual-level migrants are shown with arrows in Fig. 1b. Note that in this figure, lines of migration are only drawn among counties where (1) individuals were assigned as migrants among these locations by BAYESASS and (2) they were assigned to the cluster where the arrow originates by BAPS, but sampled in the county where the arrow points.

Migration covariates

Leave-one-out cross-validation revealed that the model-averaged Bayesian GLMs for predicting migration had good predictive capacity, demonstrated by a high correlation between values predicted from the model and those observed for both immigration (Spearman's rank correlation coefficient $r_s = 0.91$) and emigration ($r_s = 0.93$). Migration into a county was positively associated with *pig farms* and *game farms* ($\Pr(\beta_i > 0) = 1$, for both parameters; Table 1). For an increase in 10 *pig farms* within a county, there was an 11% increase in the probability of immigration, and for an increase in 10 *game farms*,

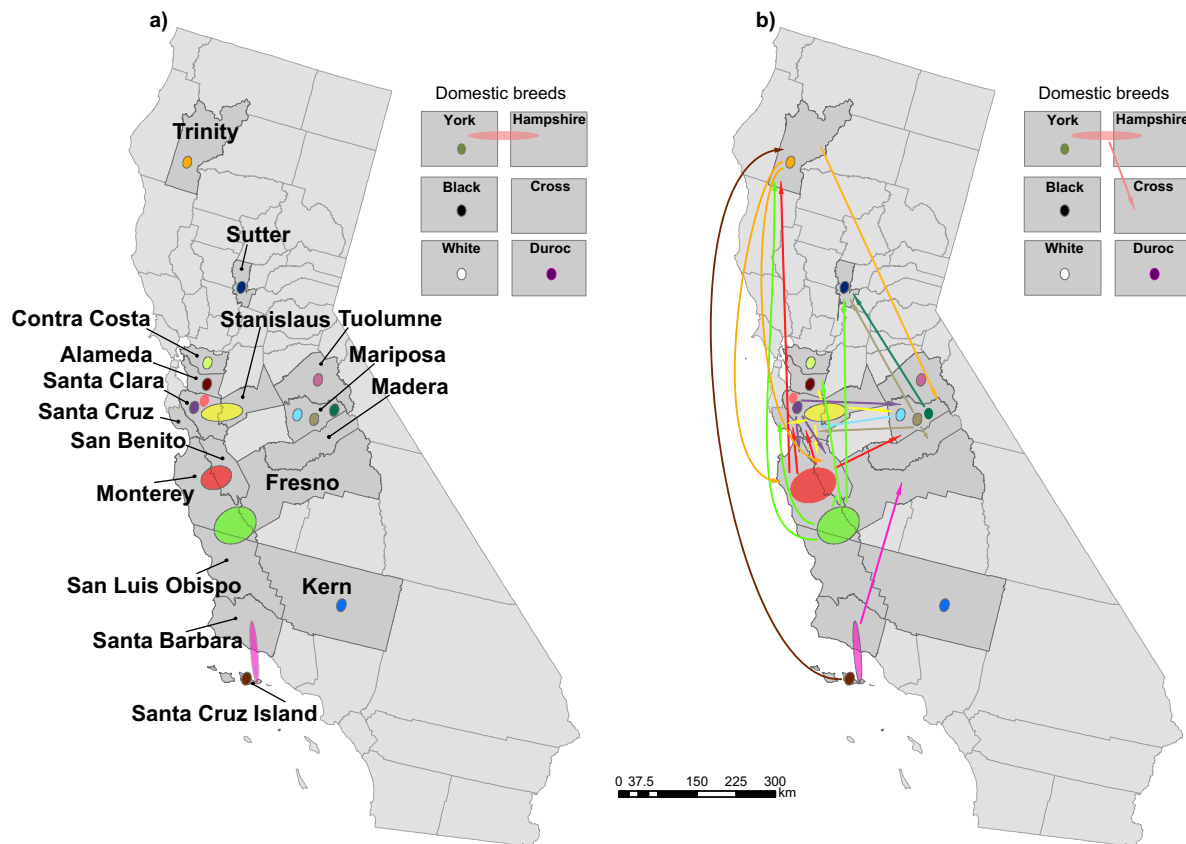


Fig. 1. Results from two Bayesian clustering analyses identified 21 genetic clusters in California. (a) Genetic clusters (ellipses) were generally found in only one county (and multiple clusters occurred within counties), with a few exceptions (ellipses overlapping county borders). (b) Arrows indicate individuals that were classified as migrants by BAYESASS and individuals who were assigned to the cluster where the arrow originates by BAPS, but captured in the county where the arrow terminates. Five genetic clusters included only domestic breeds of pigs, which did not have significant migration with wild pigs at the individual level. However, at the population level, 12.5% ($\pm 9.7\%$) of the individuals in Trinity County were identified as migrants from domestic breeds by BAYESASS.

there was a 10% increase in immigration probability. The model-averaged effect of *public index* was weak, but the median of the posterior distribution of β_i was positive in all of the best models ($\Delta\text{WAIC} < 5$). Migration out of a county was positively associated with *hunter harvest* ($\text{Pr}(\beta_i > 0) = 1$). For an increase in 10 wild pigs harvested by hunters within a county, there was a 12% increase in the probability of emigration. The model-averaged effect of game outfitters was not as strong (Table 1), but this covariate was found in all of the best models ($\Delta\text{WAIC} < 5$) and the median of the posterior distribution of β_i was positive in all candidate models. When we

predicted the probability of immigration and emigration for each county based on these model-averaged covariate estimates, areas with a high probability of movement were identified (Fig. 2). For example, there was a high probability of migration into counties in southern California (Fig. 2a) and out of counties in central California (Fig. 2b).

DISCUSSION

There was distinct population structure in wild pigs in California, with 21 populations identified in our sampling areas. This suggests that

Table 1. Bayesian model-averaged generalized linear models coefficients (β) between county-level covariates and movement into and out of counties.

Direction of movement	Parameters	Median β (95% credible interval)	$\Pr(\beta) > 0^\dagger$
Into county	<i>pig farms</i>	0.07 (0.06, 0.08)	1.00
	<i>game farms</i>	0.04 (0.04, 0.05)	1.00
	<i>public index</i>	0.01 (0.00, 0.01)	0.84
	<i>hunter harvest</i>	-0.12 (-0.13, -0.11)	0.00
	<i>game outfitters</i>	-0.05 (-0.06, -0.04)	0.00
Out of county	<i>hunter harvest</i>	0.17 (0.06, 0.26)	1.00
	<i>game outfitters</i>	0.01 (0.00, 0.02)	0.91
	<i>pig farms</i>	-0.04 (-0.05, -0.03)	0.00
	<i>game farms</i>	-0.02 (-0.03, -0.01)	0.00
	<i>public index</i>	-0.01 (-0.02, 0.00)	0.04

† Probability that $\beta > 0$ was calculated as the proportion of the posterior distribution that was greater than zero.

although wild pigs have been present in the state since the 16th century, they generally exist in small focal groups with limited geographic population ranges and do not disperse large distances. Further, we found quantifiable evidence that humans have moved wild pigs within California and identified anthropogenic factors that were associated with these translocations. Our results suggest that recreational hunting plays an important role in facilitating the spread of wild pigs. Our study is the first to predict the influence of anthropogenic factors on the intentional translocation of invasive species. We argue that future efforts to manage invasive species must consider the role of humans in dispersal.

Population structure of wild pigs in California

High levels of population structure across the sampled area ($K = 21$) and high genetic differentiation suggest that natural long-distance dispersal among wild pig populations was rare (Lowe and Allendorf 2010). Other researchers have also found low levels of dispersal or only short-range (<10 km) dispersal in wild pig populations worldwide (Hampton et al. 2004, Fulgione et al. 2016, Morelle et al. 2016). As evidence for translocation, individual-level migration indicated long-distance migration beyond that expected from natural dispersal or range expansion. For example, some individuals in Trinity County were migrants, or descendants of migrants from Monterey County (minimum distance of 355 km), San Benito County

(360 km), and Santa Cruz Island (710 km; Fig. 1b). Because previous studies have reported that most natural dispersal ranges from 4 to 10 km, with long-range dispersal ranging from 30 to 60 km (Truvé et al. 2004, Keuling et al. 2010, Morelle et al. 2016), we interpret these long-distance movements as evidence of human-mediated movement (Keuling et al. 2010, Hone 2012).

Anthropogenic translocation of wild pigs

We quantified the association between wild pig movement and anthropogenic factors to explain the evidence of translocation in California. Here, we propose potential mechanisms that could lead to the observed relationships. We found that wild pig emigration from counties was positively associated with hunter harvest and the number of licensed game outfitters (Table 1). We hypothesized that hunter harvest was a surrogate for the density and availability of wild pigs for movement, as well as interest in hunting wild pigs. The positive relationship between emigration and this covariate may indicate that these higher-density populations of wild pigs provide a source for capture and transport to new areas by hunters or outfitters. This hypothesis was also supported by the relationship between emigration and the number of game outfitters, a covariate considered to represent the size of, and demand for, the recreational hunting industry in a county.

Furthermore, we found that the number of game farms, the number of domestic pig farms, and the amount of public land were positive predictors of immigration into counties (Table 1). The number of game farms in a county is a surrogate for the size of the game farm industry, and the size of this industry is associated with wild pig hunting. Domestic pig farms might serve as local sources of wild pigs due to either escape (Goulding 2001, Morelle et al. 2016) or intentional release for hunting purposes (Spencer and Hampton 2005, Scandura et al. 2008, Morelle et al. 2015). This relationship is also supported by our observation that in one of the counties identified as a common recipient of wild pigs at the individual level (Trinity County; Fig. 1b), immigrants were identified at the population level from two domestic breeds (Appendix S4). Our findings support reports that sport hunters in California released pigs on public land in order to promote

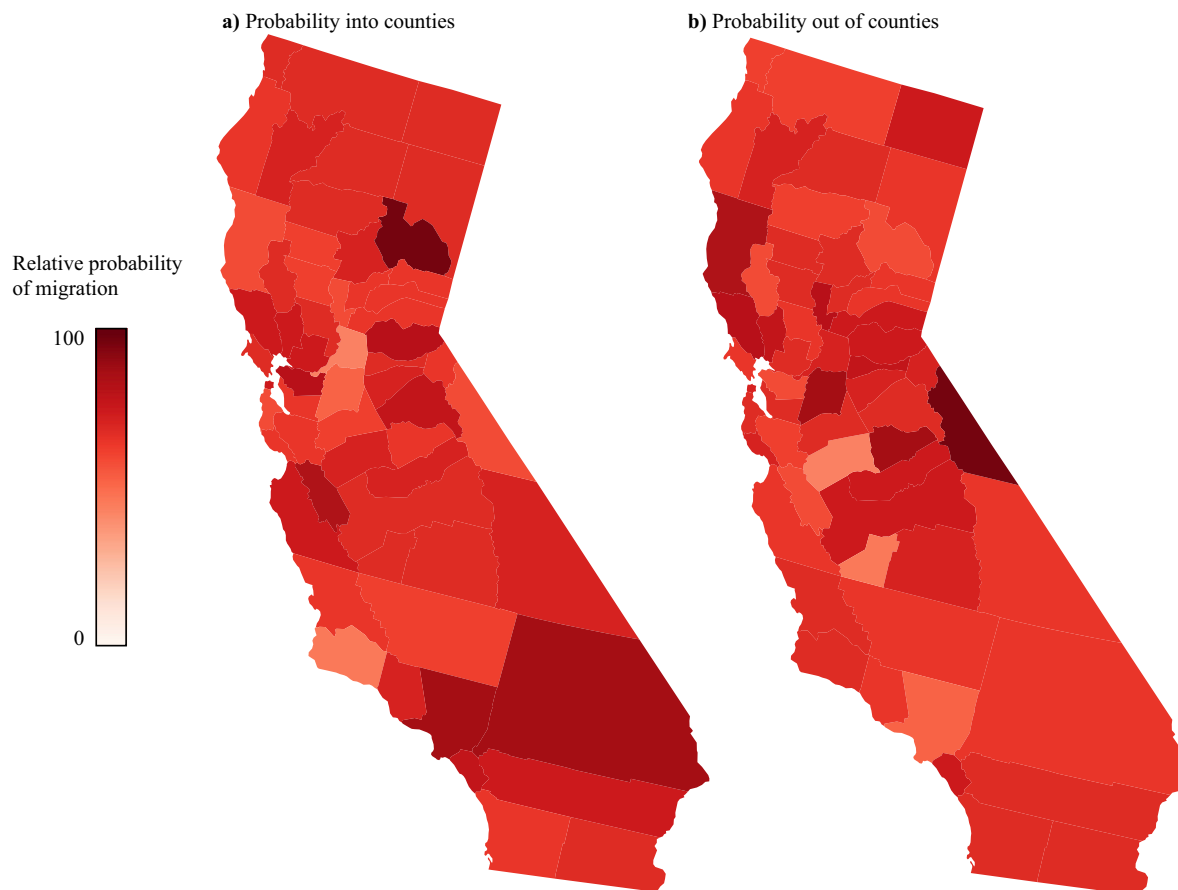


Fig. 2. Relative probability of migration into (a) and out of (b) each county in California based on model-averaged estimates from Bayesian generalized linear models (see *Methods* for a description of predictor variables used in analysis). Darker colors represent a higher probability of migration, while lighter colors represent a lower probability of migration.

populations for hunting in new areas (Pine and Gerdes 1973, Waithman et al. 1999).

Limitations of this study

In an ideal study, we could conduct a replicated, randomized experiment in which the genomes of populations were observed with and without planned translocation events. Since translocation of pigs is unethical and illegal, such a study is not possible. Instead, our study is a correlative one, in which we based inference on observations of migration given genetic data and societal covariates. Samples were collected opportunistically, instead of randomly, so it is possible that there was an effect of sampling on inference. Since genetic sampling was opportunistic, we did

not necessarily achieve a demographic distribution (age and sex of individuals) that is identical to wild populations. However, it is unlikely that there would be an effect of demography on inference, as analyses extend multiple generations into the past and there is no known effect of sex on translocation probability. Additionally, this approach allowed us to take advantage of a much larger data set (with more samples and geographic breadth) than if we used only samples from an empirically designed study, an approach commonly utilized in genetic studies (Matala et al. 2014, Mandeville et al. 2015). Nevertheless, we must view our results with the caveat that the results could appear different if populations were sampled randomly.

Since our results are based on the linkage of genetic data and societal covariates, we must have constraints on inference. Some of the societal covariates (i.e., *public index* and *game outfitters*) that were linked to translocation of wild pigs in California had small effect sizes (the 95% CIs of coefficients were close to zero; Table 1). There are a number of potential explanations for the small effect sizes of these covariates. Because data that directly describe intentional capture and translocation of wild pigs are not available, we used covariates that were proxies for the mechanisms we hypothesized to underpin wild pig translocation. For example, *game outfitters* is the number of outfitters who registered with the State of California and represented a measure of the hunting industry. There are presumably other businesses that escaped our analyses that may serve as better measures of recreational hunting. More broadly, there are likely other mechanisms important for translocation of wild pigs. Due to a lack of exact geographical sampling locations and the coarse nature of the covariates analyzed, we aggregated samples to the county level. We were not able to use a traditional landscape genetics approach (i.e., we could not evaluate the effects of habitat features of the landscape on population structure and migration), as geographic features vary greatly within counties, and samples could have been collected from various locations within the counties. Instead, we used county-level covariates. The county-level scale provides imprecise values for both covariates and migration rates, which might have produced additional uncertainty in the data. Nevertheless, even using these coarse-level data, we found significant results and the models were good at predicting migration (based on cross-validation), which suggests that (1) these covariates are good at predicting human-mediated dispersal and (2) further research might help define these relationships. As an increasing number of wild pig samples become available for genetic analyses (A. J. Piaggio, *unpublished data*), we recommend further testing of these hypotheses.

Additionally, the covariate data were collected on different temporal scales, which was not the exact same temporal range when sampling was conducted. We highlight that these covariates were not perfect estimates of the anthropogenic processes that we analyzed. However, these were

the relevant data that were available and we considered that estimating the mean of these covariate values across several years was suitable for examining the cultural trends associated with these factors around the time of genetic sampling. Despite these limitations, our analyses had strong predictive capacity (given cross-validation analysis) for movement of wild pigs among counties in California.

Implications for management

The dichotomy between low natural dispersal and long-distance human movement is an important result for efforts to manage and mitigate the damage caused by this species. Through intensive genetic sampling in specific regions of interest, future researchers could use the tools and results documented here to identify “eradication units”: populations that are linked by dispersal, but isolated from potential re-invasion sources (Robertson and Gemmell 2004). By defining eradication units, managers can systematically eradicate invasives from specific regions while reducing the risk of re-invasion following eradication (Tabak et al. 2015). If we focus only on natural dispersal and assume that wild pigs can move a maximum of 60 km between genetic clusters (Truvé et al. 2004), we could infer the existence of eradication units. However, for wild pigs and for other commonly moved invasive species, managers must consider the potential for human-assisted translocation when planning eradication efforts, as an individual could be moved to a previously eradicated area. Translocation of invasives also has important implications for disease management, as the introduction of one exposed or infected individual can have significant consequences for disease spread to wildlife and livestock populations (Wyckoff et al. 2009). Our method of identifying potential source locations (Fig. 2b) can help managers evaluate and mitigate the risk of translocations.

This is the first analysis we are aware of that attempts to estimate the societal drivers of the intentional release of invasive species. Understanding the underlying mechanisms driving human translocation and release of invasive species can be used to develop policies that reduce these risks. For example, there has been ongoing debate regarding managing wild pigs as a big game mammal in California (Tietje and Barrett

1993, Zivin et al. 2000). Although hunting removes animals from the burgeoning statewide wild pig population (Sweitzer et al. 2000), our results indicate that hunter interest in harvesting them is facilitating their expansion into new areas. Decisions on how best to manage invasive species, in light of human-mediated translocation, should be balanced by both the positive and negative repercussions of resource policy.

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