

Transient population dynamics drive the spread of invasive wild pigs in North America

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1 **Abstract**

2 Invasion of nonindigenous species is considered one of the most urgent problems affecting
3 native ecosystems and agricultural systems. Mechanistic models that account for short-term
4 population dynamics can improve prediction because they incorporate differing demographic
5 processes that link the environmental conditions of a spatial location explicitly with the invasion
6 process. Yet short-term population dynamics are rarely accounted for in spatial models of
7 invasive species spread.

8 Accounting for transient population dynamics, we predict the population growth rate and
9 establishment probability of wild pigs following introduction into any location in North America.
10 We compared predicted population growth rate with observed geographic rates of spread and
11 found significant relationships between the annual rate of spread and population growth rates.

12 We used geospatial data on the distribution of mast producing tree species (a principle forage
13 resource of wild pigs) and agricultural crops that can replace mast in their diets to predict
14 population dynamics using transient population simulations. We simulated populations under
15 different initial population sizes (i.e. number of introduced individuals, often termed propagule
16 size) and for different amounts of time following introduction. By varying the initial population
17 size and simulation time, we were able to identify areas in North America with high probability
18 for establishment of wild pigs if introduced. Our findings can be used to inform surveillance and
19 removal efforts to reduce the potential for establishment and spread of wild pigs.

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21

22 Introduction

23 Invasion of nonindigenous species is considered one of the most urgent problems affecting
24 native ecosystems with 87% of imperiled species threatened by invasive species (Mack et al.,
25 2000; McClure et al., 2018). Additionally, nonindigenous species threaten agricultural systems
26 requiring considerable policy activity to mitigate invasive species concerns (Miller et al., 2018;
27 Miller, 2020). Existing theory indicates that the distribution and spread of invasive species is the
28 result of complex ecological processes that include the frequency and size of introduction
29 (propagule pressure), species-specific traits that provide a fitness advantage (high reproductive
30 capacity and dispersal), and biotic and abiotic characteristics of the recipient ecosystem that limit
31 or facilitate invasion (Simberloff, 2009; Lustig et al., 2017). However dynamic risk assessments
32 of establishment and spread typically lack explicit consideration of these interacting factors
33 (Catford et al., 2011; Gallien et al., 2015) and broad scale projections of invasive species
34 distributions are typically based on static approaches linking species occurrence to biotic and
35 abiotic factors (Guisan and Zimmermann, 2000; Lustig et al., 2017). Mechanistic models that
36 account for short-term population dynamics can improve prediction because they incorporate
37 differing demographic processes that link the environmental conditions of a spatial location
38 explicitly with the invasion process. Yet short-term population dynamics are rarely accounted for
39 in spatial models of invasive species spread (Lustig et al., 2017).

40 When populations are not at equilibrium (e.g., the age structure is not the stable age structure and
41 population growth are not defined by the equilibrium population growth rate, λ), they are
42 expected to exhibit transient dynamics (Caswell and Werner, 1978; Hodgson and Townley,
43 2004; Tremblay et al., 2015). Transient dynamics can cause populations either grow or shrink at
44 a much faster rate than would be expected under equilibrium conditions (Stott et al., 2011;
45 McDonald et al., 2017). When a small group of conspecific individuals is introduced to a new
46 location (a “propagule”), it is not likely to be a stable population, and transient dynamics can
47 lead to either rapid growth and establishment of a population or local extinction (Iles et al.,
48 2016).

49 Invasive wild pigs (*Sus scrofa*), also known as feral hogs, feral swine, or wild boar, are
50 recognized as one of the most widespread and destructive invasive species in the world (Barrios-
51 Garcia and Ballari, 2012). Wild pigs are native to Eurasia and Northern Africa, but have been
52 widely introduced for centuries, often deliberately, and now occupy every continent except
53 Antarctica (Mayer and Brisbin, 1991; Lewis et al., 2017). In North America it is an extremely
54 destructive invasive species that is of concern for human and animal health (Miller et al., 2017),
55 causes significant economic damage (Anderson et al., 2016), negatively impacts imperiled
56 species (McClure et al., 2018), and is commonly introduced into new locations (Tabak et al.,
57 2016; Hernandez et al., 2018). These concerns have generated significant Federal policy to
58 mitigate these impacts with the US Department of Agriculture establishing the Animal Plant
59 Health Inspection Service (APHIS) National Feral Swine Damage Management Program in 2013
60 (federal government fiscal year 2014) aimed at reducing the spread of wild pigs in the United
61 States (USDA, 2015; Miller et al., 2018). Nevertheless, the distribution of wild pigs in Canada
62 and the United States has increased dramatically in recent years (Michel et al., 2017; Snow et al.,

63 2017), and research suggests that a major mechanism for their spread is translocation of
64 individuals to augment populations for recreational hunting (Tabak et al., 2016). Wild pigs
65 evolved as pulsed resource consumers of mast crops; they have larger litter sizes and reproduce
66 more often under favorable forage conditions, and have reduced fecundity under poor forage
67 conditions (Ostfeld and Keesing, 2000). This elasticity in fecundity makes wild pigs especially
68 susceptible to transient dynamics (Bieber and Ruf, 2005; Tabak et al., 2018). Despite their
69 ancestral dependence on mast crops, wild pigs have evolved to be dietary generalists, as
70 agricultural crops can replace mast in their diets (Schley and Roper, 2003; Rosell et al., 2012)
71 and they currently thrive in ecosystems that lack mast producing species (Caley, 1997;
72 Choquenot and Ruscoe, 2003). Nevertheless, their reproductive biology retains this elasticity of
73 fecundity, which can cause populations to rapidly grow and establish following introduction in
74 new environments, leading to the further expansion of this species. Despite significant efforts to
75 forecast the spread of wild pigs (Snow et al., 2017), estimate the probability of occurrence
76 (McClure et al., 2015), and predict the potential density of wild pig populations (Lewis et al.,
77 2017) there are no available spatial predictions of population growth and establishment risk if
78 wild pigs were released into a given spatial location.

79 Our objective was to predict the population growth rate and establishment probability of wild
80 pigs (accounting for transient dynamics) following introduction into any location in North
81 America. We then compared predicted population growth rate with observed geographic rates of
82 spread to determine if increased population growth was associated with increased spread (e.g.
83 invasion). We used geospatial data on the distribution of mast producing tree species (a principle
84 forage resource of wild pigs) and agricultural crops that can replace mast in their diets to predict
85 population dynamics using transient population simulations. We simulated populations under
86 different initial population sizes (i.e. number of introduced individuals, often termed propagule
87 size) and for different amounts of time following introduction. By varying the initial population
88 size and simulation time, we were able to identify areas in North America with high probability
89 for establishment of wild pigs if introduced. Our findings can be used to inform proactive
90 surveillance and removal efforts to reduce the potential for establishment and spread of wild
91 pigs.

92 **Methods**

93 *Predicting population growth and establishment*

94 We used transient population dynamics models to simulate population trajectories for invasive
95 wild pig populations under different types of environments that they could potentially experience
96 in North America. Survival and fecundity rates for different mast qualities (poor, intermediate,
97 and good) were obtained from the literature (Briedermann, 1967; Bieber and Ruf, 2005). Data
98 are scarcely available for the quality of mast from trees over time. In the literature we found
99 historic data from one common mast species, *Fagus sylvatica*, over 114 years (Hilton and
100 Packham, 2003) and from a community of five mast tree species, *Quercus* spp., over 12 years
101 (Koenig et al., 1994). Following Tabak et al. (2018), we used these historic mast data to simulate
102 three broad types of environmental conditions to which wild pigs might be introduced: an
103 environment with one mast tree species, an environment with a mast community (containing five

104 mast tree species), and an environment with agricultural subsidy. We conducted simulations in
105 these three environments under nine different introduction scenarios: we used propagule sizes of
106 5, 10, or 20 as the number of females introduced at the beginning of the simulations, and for each
107 of these propagule sizes, we allowed simulations to run for 1, 5, or 10 years.

108 We estimated stochastic population growth rate (λ_s) and probability of establishment for wild pig
109 populations in these environments and in environments with agricultural subsidy using the
110 methods and the R scripts of Tabak et al. (2018). A simulated population was determined to have
111 established if $\lambda_s > 1$ and population size at the end of simulation was ≥ 60 . Tabak et al. (2018)
112 provide justification for using 60 individuals as the threshold for population establishment in
113 wild pig populations. Unfortunately, data are unavailable for mast records from areas with 2-4
114 mast species and from areas with > 5 mast species. Therefore, we assumed that five mast species
115 represented the maximum population growth potential resulting from their consumption of mast
116 crops. For areas with 2-4 mast species, we estimated λ_s and establishment probability using loess
117 regression, where the predictor variable was the number of mast species (1 or 5) and the response
118 variable was λ_s or establishment probability. To calculate the λ_s in areas with both mast and
119 agriculture, we estimated λ_s as the mean between the growth rate estimated as a result of mast
120 and the growth rate estimated as a result of agricultural subsidy. To calculate establishment
121 probability in such situations, we took the sum of probability of establishment that was estimated
122 as a result of mast species and that resulting from agricultural subsidy.

123 There are clearly limitations in our estimation of growth rate and of establishment probability as
124 we extrapolated to areas with numbers of mast trees for which we do not know the frequency of
125 mast and we are unaware of how wild pig growth potential changes in the presence of both
126 agriculture and mast trees. We also only considered the effects of forage on population growth,
127 but other factors might affect growth rate (e.g., climate could have strong effects on survival).
128 However, we are interested in the general trends of population growth and establishment across
129 the continent more than precisely estimating these rates.

130 To apply these growth rates and establishment probabilities to geographic locations, we used a
131 geospatial layer depicting the number of mast species in each 1 km² (Burdett et al. unpublished
132 data) and the presence of crops that can replace mast in wild pigs' diets using the USDA's
133 cropscape data (NASS, 2019). Cropscape data are only available for USA, and we wanted to
134 extend our model results to all of North America, so we also used the consensus land cover
135 layer for North America (Tuanmu and Jetz, 2014) and compared this with the results in USA that
136 were produced using the detailed cropscape data (Fig S3). Since the maps created using these
137 two datasets were similar for the USA, we assume that it is reasonable to use the consensus land-
138 cover and apply our results to all of North America.

139 *Determining rates of spread*

140 We estimated the geographic rate of spread of wild pigs in the contiguous U.S. using data from
141 the National Feral Swine Mapping System (Corn and Jordan, 2017). These data describing wild
142 pig distribution were compiled at irregular intervals from 1982-2008 and annually since 2008.
143 They are the best available data describing the known distribution of wild pigs over the past 36

144 years and have been used to forecast the spread of wild pigs (Snow et al. 2017), estimate the
145 probability of occurrence (McClure et al. 2015), determine wild pig agricultural damage risk
146 (Miller et al. 2017), predict federal policy to control wild pigs (Miller et al. 2018), and determine
147 the risk wild pigs pose to imperiled species (McClure et al. 2018). Polygons representing the
148 known geographic extent of established wild pig populations (defined as populations present for
149 two or more years with evidence of reproduction) are reported to the National Feral Swine
150 Mapping System nationally by wildlife professionals in state wildlife resource agencies and the
151 United States Department of Agriculture. The resulting distribution data is curated for accuracy
152 with national data available annually.

153 Polygons representing the observed distribution for 1982, 1988, 2004, 2008, 2013, and 2017
154 were aggregated to watersheds (HUC12) as described in McClure et al. (2015) to discretize
155 consistent, comparable, and ecologically relevant sampling units. The annual watershed rate of
156 spread among HUC12 watersheds was then calculated for three coarser watershed scales –
157 HUC4, HUC6, HUC8. This was done because the spatial scale used for analysis can influence
158 inference (Farnsworth et al. 2006). We calculated the annual rate of spread (θ) for each
159 watershed j in each time period t as,

$$\theta_{j,t} = \frac{\eta_{i,t+1} - \eta_{i,t}}{T}$$

160 Where $\eta_{i,t}$ is the count of HUC12 watersheds occupied by wild pigs in the coarser watershed j in
161 year t , and T is the number of years between t and $t + 1$. We also calculated the mean annual
162 rate of spread from 1982 to 2013, the final year in this range was the beginning of a National
163 Feral Swine Damage Management Program to control wild pigs, and from 2013 to 2017 which
164 represents the period after the National program began.

165 To determine if the predicted population growth rate was associated with the annual rate of
166 spread (θ) in watersheds we regressed the annual rate of spread, θ , on the mean watershed
167 population growth rate, λ_s . This was implemented using a linear model assuming a Gaussian
168 error structure. We used adjusted R^2 as a measure of goodness of fit and the predictive capacity
169 of each model (Kutner et al., 2005).

170 **Results**

171 Our spatial estimates of λ_s that used the detailed cropland data for the US were similar to
172 estimates using the cultivated layer that is available for all of North America (Fig. 1). Since these
173 estimates were similar and using the cultivated data allows our results to have broader
174 interpretation, we focus on the continental scale for the remainder of this article. With a small
175 initial population size (propagule size = 5), mean λ_s was < 1 , regardless of the number of years
176 in which we allowed simulations to run following introduction (Fig. 1). As we increased
177 propagule size and the number of years of simulation, λ_s increased so that with a propagule size
178 of 20 and ten years of simulation, λ_s was > 1 for almost all of North America. We found the
179 highest growth rates in the upper Midwestern United States and the southern prairie region of
180 Canada.

181 The mean establishment probability was very low ($< 6\%$) when the initial population size was 5
182 females (Fig. 2). When propagule size was increased to 20 and simulations ran for 5 to 10 years,
183 establishment probabilities were high in the same locations we found the highest growth rates
184 (Figure 1 and 2). Establishment probabilities approached 1 for many locations in the upper
185 Midwestern US.

186 *Annual spread rate*

187 The annual spread rate (θ) was proportionally consistent across the three watershed scales
188 however it demonstrated strong spatial heterogeneity (Figure 3, see supplemental for all
189 watershed scales). Mean annual rates of spread changed among time periods with the greatest
190 rates of spread occurring from 1988 to 2004 across all watershed scales ($\theta_{HUC4}=4.54$, $\theta_{HUC6}=2.86$,
191 $\theta_{HUC8}=0.65$) (see supplemental for all spread rates). Annual rates of spread demonstrated spatial
192 heterogeneity and were not constantly greatest along the northern extent of wild pig distribution.
193 During the earliest periods from 1982 to 2004 spread rates were positive across the majority of
194 the wild pig distribution. From 2004 to 2013 watersheds along the Red River, Rio Grande River,
195 and Ohio River consistently had the highest spread rates. Annual spread rates declined
196 significantly across all watershed scales after the establishment of the National Feral Swine
197 control program in 2013 with some regions having negative spread rates. The highest rates of
198 spread after 2013 were confined to the Ohio River and Tennessee River watersheds.

199 *Association of spread rate and population growth rate*

200 We found significant relationships between the annual rate of spread and population growth
201 rates. From 1982 to 2013, the period prior to the National Feral Swine control program,
202 population growth rates were a significant positive predictor of the annual rate of spread for all
203 watershed scales (Fig. 4). The mean population growth rate explained a large amount of the
204 variation in rate of spread with adjusted R^2 values ranging from 0.729 to 0.953 for the periods
205 from 1982 to 2013 (see supplemental Table S2). Additionally, the effect of population growth
206 rates on spread rates increased 47.6% (HUC4), 53.2% (HUC6) and 54.6% (HUC8) from the
207 earliest period (1982 to 1988) to the period just prior to the program (2008 to 2013). For the
208 period after the establishment of the Feral Swine control program (2013 to 2017), population
209 growth rates were a significant positive predictor of the annual rate of spread only at the HUC8
210 watershed scale.

211 **Discussion**

212 Explicitly accounting for initial population size and age structure allowed us to account for
213 transient dynamics and demographic stochasticity that influence predictions of population
214 growth and probability of establishment. Our geospatial projections of population growth rate
215 and establishment probability (Figs. 2 and 3) highlight areas at increased risk of successful
216 establishment of wild pig populations if introduced. The strong correlation between our estimates
217 of population growth (λ_s) and the annual watershed rate of spread (θ) supports the validity of our
218 population growth estimates. In other systems, transient population growth rate has been
219 identified as important in predicting establishment success and long term viability of invading
220 species (Iles et al., 2016). Our results can be used to target areas for surveillance that have higher

221 potential for wild pig establishment and rapid population growth allowing for early identification
222 of wild pigs, as well as efforts to minimize population expansion once new wild pig populations
223 are identified.

224 *Applying mechanistic models to geospatial projections*

225 While mechanistic models are often used for distribution and niche modeling for invasive
226 species (Kearney and Porter, 2009; Peterson et al., 2015), population dynamic processes across
227 spatial scales are more commonly evaluated using statistical models to correlate population
228 processes with spatial covariates (but see Chandler et al., 2018; Quintana-Ascencio et al., 2018).
229 Correlative spatial models are convenient, especially in systems with less biological data,
230 because they do not require an understanding of the mechanistic links between an organism and
231 its environment. However, mechanistic processes tend to limit the expansion of species
232 distributions, so it can be useful to build models that evaluate mechanistic processes across large
233 spatial extents when the goal is to predict the growth and establishment potential of a species.
234 Furthermore, for populations that experience transient dynamics, mechanistic models may be
235 more applicable than correlative statistical models. When a population is introduced into a new
236 environment, it will usually exhibit transient dynamics (Iles et al., 2016) and wild pigs are
237 especially prone to transient dynamics due to their evolution as pulsed resource consumers
238 (Bieber and Ruf, 2005; Tabak et al., 2018).

239 *Comparison to other studies*

240 Our estimates of population growth and establishment probability correspond well to the
241 reported establishment of wild pigs throughout the United States and the prairie provinces of
242 central Canada (Michel et al., 2017). However, our estimates of establishment probability differ
243 in several ways from the predicted spread of wild pigs in the United States (Snow et al., 2017).
244 We found high establishment probability throughout the upper Mississippi and Ohio River
245 drainages while previous studies predicted lower probability of spread in these areas. The
246 historical spread of wild pigs in the United States by Snow et al. (2017) implicitly includes
247 factors such as human translocation of wild pigs which previous studies have found to be
248 important in the spread of wild pigs (Tabak et al., 2016). The differences between Snow et al.
249 (2017) and our results may stem from differences in the frequency of introduction, which is
250 likely driven by anthropocentric factors. This indicates that while the probability of
251 establishment is generally high in some regions of the U.S., the historical frequency of
252 introduction has likely been low. Our predicted probability of establishment and population
253 growth rates generally correspond well with the predicted equilibrium population density of wild
254 pigs by (Lewis et al., 2017).

255 The differences among the predictions of wild pig spread (Snow et al., 2017), population density
256 (Lewis et al., 2017), and probability of establishment (McClure et al., 2015) are not mutually
257 exclusive. The differences among these results is largely due to each study focusing on a
258 different component of the invasion process - introduction, establishment, population growth,
259 and spread (Reise et al., 2006). These differences highlight the need to develop integrated
260 mechanistic approaches that explicitly include factors that drive introduction pressure (e.g. Snow

261 et al. (2017) and Tabak et al. (2016)) probability of establishment and population growth (e.g.
262 our study), and factors regulating long-term population growth and equilibrium population size
263 (e.g. Lewis et al., 2017). Accounting for the invasion process in a spatially explicit context would
264 allow for greatly improved predictions of establishment risk and consequences once established.

265 *Management implications*

266 Establishment probability was very low when initial population size was small and when
267 populations had fewer years to become established (Fig. 3), because populations in these
268 simulations were unlikely to meet one of the criteria for establishment: a population size of 60
269 individuals in the final simulation year. This indicates that there may be the opportunity to
270 prevent population establishment if actions are undertaken quickly upon recognizing newly
271 introduced populations. With larger initial populations and more time following introduction, the
272 potential for population establishment increased dramatically, indicating that it is best to prevent
273 introductions of large numbers of individuals and to begin interventions early. Reducing the
274 frequency and size (number of animals) of releases of wild pigs can reduce establishment
275 probability, but these goals may be difficult to implement, as movement and release of wild pigs
276 is common and has been documented on multiple continents (Hampton et al., 2004; Tabak et al.,
277 2016; Hernandez et al., 2018). This is often complicated by limitations of current tools available
278 for detecting newly released pigs. Tools such as pig detection dogs (Keiter et al., 2016) and
279 passive monitoring using camera traps (Tabak et al., 2019) are difficult to deploy over large
280 geographic extents for long periods of time. Our results can be used to refine where monitoring
281 using these tools is conducted, improving the chances of early detection of pigs. When
282 considering management to prevent population establishment, it is important to note that our
283 methods only account for a single introduction event so likely represent a conservative estimate
284 of establishment probability. Wild pigs are often repeatedly introduced to the same location
285 (Mayer and Brisbin, 1991), which can increase establishment probability through demographic
286 rescue of the founder population (Hufbauer et al., 2015).

287 *Extensions*

288 Our method of estimating population growth and establishment success has some important
289 limitations that offer opportunities to extend our approach. Complete data on the frequency and
290 intensity of mast and how this changes with the size and community structure of mast species is
291 limited or not available. To address this data limitation we extrapolated using available data,
292 however there is uncertainty in our approach for making this extrapolation. The development of
293 data describing mast frequency and intensity over large geographies in North America would
294 have significant value for population dynamic modeling of many species that consume seasonal
295 mast and fruit. Additionally, we used data linking how mast frequency and intensity affect vital
296 rates of wild pigs from Europe (Briedermann, 1967; Bieber and Ruf, 2005); data describing this
297 relationship in other continents are needed to better extrapolate globally. In our predictions the
298 primary driver of wild pig vital rates was assumed to be access to mast. However, previous
299 studies have indicated that precipitation and temperature can influence survival of younger age
300 classes impacting transient population dynamics of wild pigs (Miller, 2017). Currently most
301 studies reporting survival, litter size, and frequency of litters and how these factors correlate with

302 environmental conditions are from wild pig populations in Europe. Studies collecting these vital
303 rates for wild pig populations in North American would be of great value. We also do not
304 account for inter and intra species interactions that may also be limiting for founder populations.
305 For example Lewis et al. (2017) found that predator species richness was negatively associated
306 with wild pig population density. Accounting for these interactions within a dynamical modeling
307 framework that accounts for transient dynamics would be an exciting extension of our work.
308 Despite these limitations, predicted population growth and the spread rate of wild pigs in areas
309 where they have been introduced were highly correlated. The positive correlation indicates that
310 despite the data uncertainties, our projections are reasonable estimates of population growth and
311 establishment potential for wild pigs.

312 *Conclusion*

313 Risk assessments of establishment and spread of invasive species that consider the frequency and
314 size of introduction along with the biotic and abiotic characteristics of the recipient ecosystem
315 using mechanistic models that account for short-term population dynamics can improve
316 prediction. Accounting for short-term population dynamics in spatial models of invasive species
317 spread will become increasingly important as variation in climatic conditions increases. For
318 many invasive species, including wild pigs, increasing temperature is expected to increase
319 invasion success and expand regions with the potential for invasion (Vetter et al., 2015). Spatial
320 models that account for short-term population dynamics can allow for uncertainties resulting
321 from increased climate variation to be explicitly considered, improving predictions. An
322 important extension of our work is to integrate, using mechanistic approaches that account for
323 short-term population dynamics, with ecological and anthropocentric processes that determine
324 introduction, establishment, and spread of invasive species.

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328 **FIGURES:**

329 Figure 1: Estimated transient population growth rates (λ_s) for wild pigs in North America by
330 years after introduction (x axis) and initial population size (y axis).

331 Figure 2. Estimated probability of establishment for wild pigs in North America by years after
332 introduction (x axis) and initial population size (y axis).

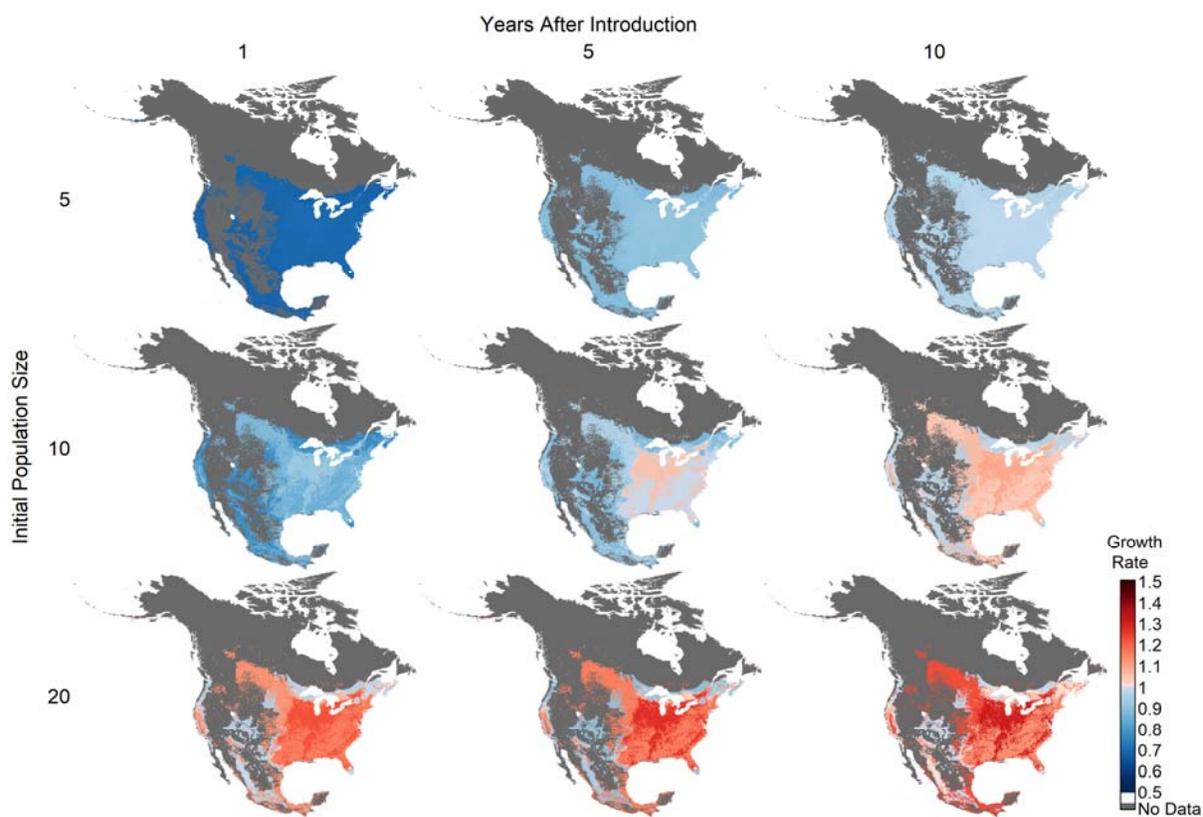
333 Figure 3. Annual watershed level spread rate (watersheds/year) for wild pigs from 1982 to 2017
334 for three watershed scales. Red indicates positive rates of spread and blue indicates negative
335 rates of spread (i.e. contractions in the number of occupied watersheds).

336 Figure 4. Regression coefficients for linear models regressing wild pig spread rate on transient
337 population growth rate. Spread rate was increasingly positively associated with transient
338 population growth rate in all time periods except the period from 2013 to 2017. A national wild
339 pig control program was initiated beginning in 2013.

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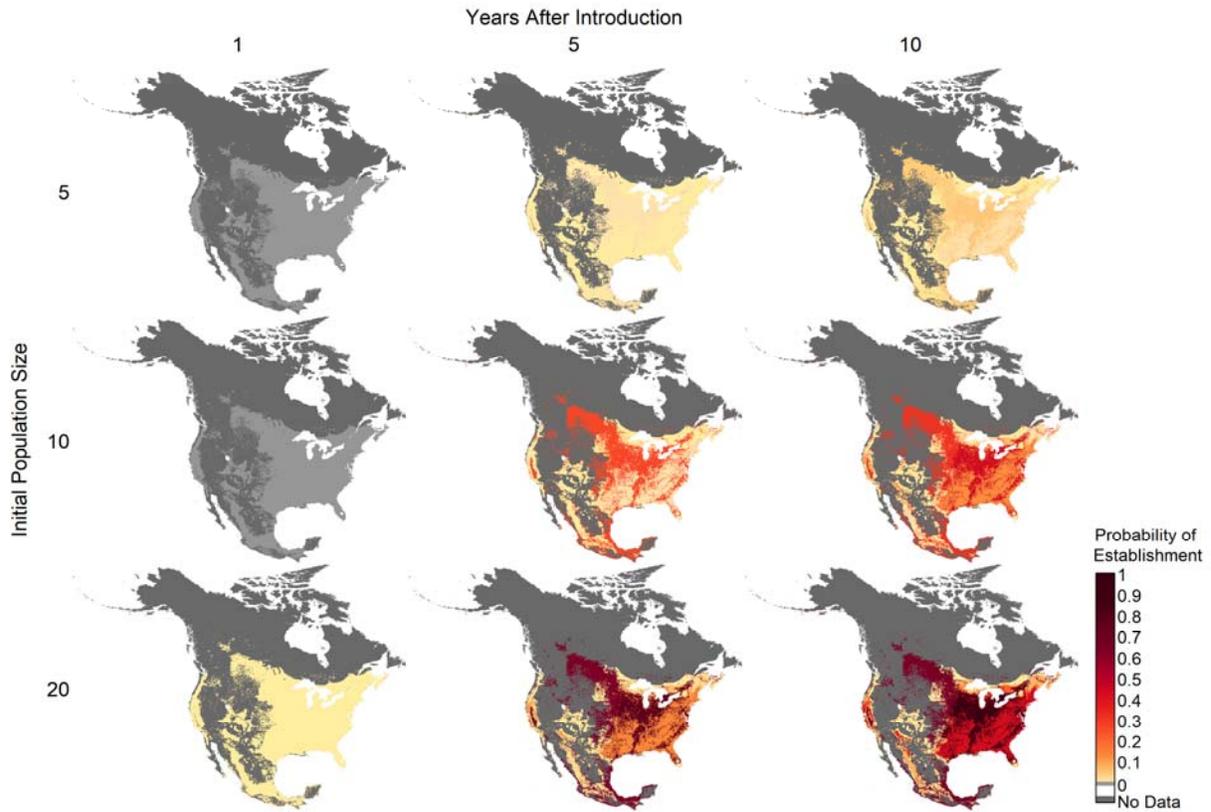
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342 Figure 1: Estimated transient population growth rates for wild pigs in North America by years
343 after introduction (x axis) and initial population size (y axis).



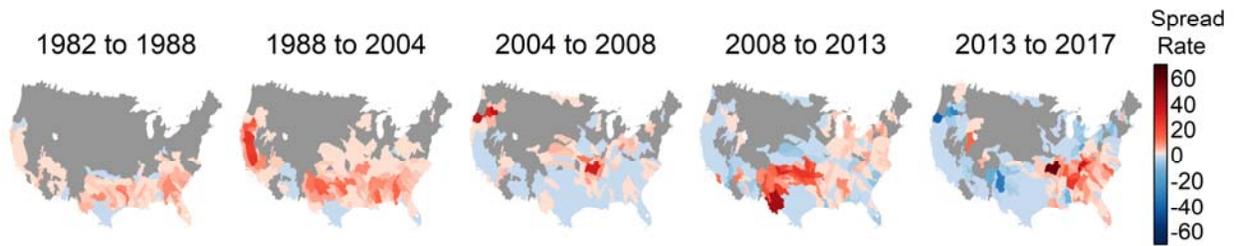
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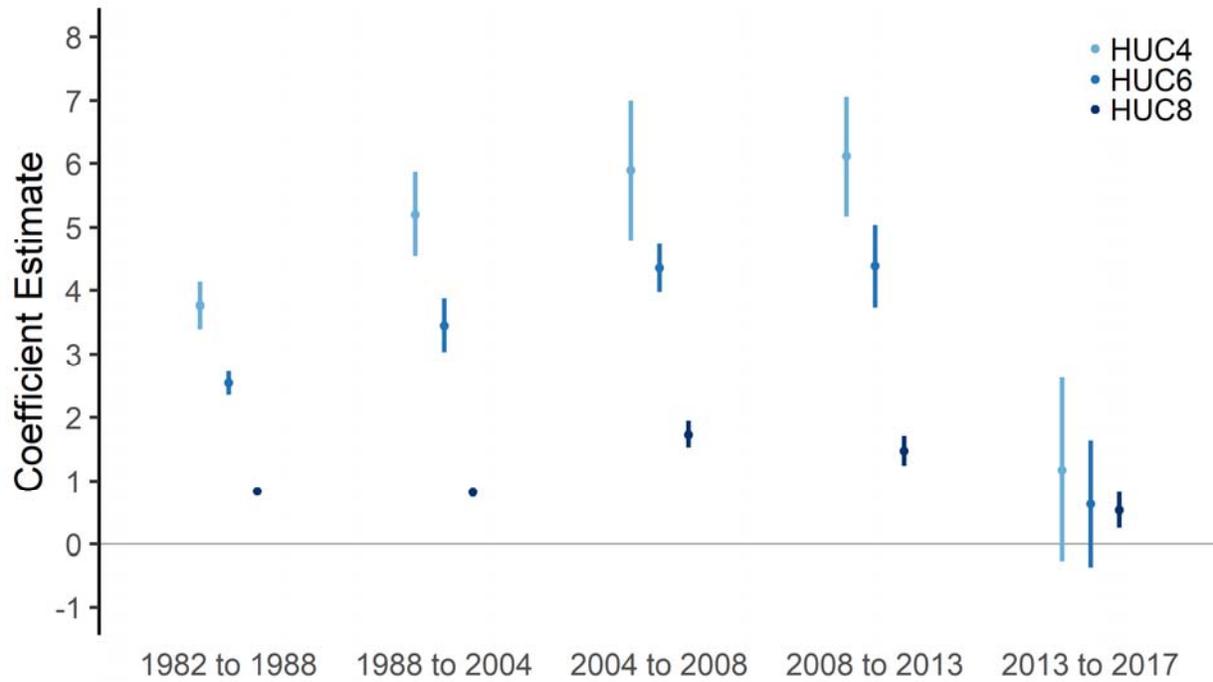
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