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# Interpreting and predicting the spread of invasive wild pigs

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## Summary

**1.** The eruption of invasive wild pigs (IWPs) *Sus scrofa* throughout the world exemplifies the need to understand the influences of exotic and nonnative species expansions. In particular, the continental USA is precariously threatened by a rapid expansion of IWPs, and a better understanding of the rate and process of spread can inform strategies that will limit the expansion.

**2.** We developed a spatially and temporally dynamic model to examine three decades (1982–2012) of IWP expansion, and predict the spread of IWPs throughout the continental USA, relative to where IWPs previously inhabited. We used the model to predict where IWPs are likely to invade next.

**3.** The average rate of northward expansion increased from 6·5 to 12·6 km per year, suggesting most counties in the continental USA could be inhabited within the next 3–5 decades. The spread of IWPs was primarily associated with expansion into areas with similar environmental characteristics as their previous range, with the exception of spreading into colder regions. We identified that climate change may assist spread into northern regions by generating milder winters with less snow. Otherwise, the spread of IWPs was not dependent on agriculture, precipitation or biodiversity at the county level. The model correctly predicted 86% of counties that were invaded during 2012, and those predictions indicate that large portions of the USA are in immediate danger of invasion.

**4.** *Synthesis and applications*. Anti-invasion efforts should focus along the boundaries of current occupied range to stop natural expansion, and anti-invasion policies should focus on stopping anthropogenic transport and release of invasive wild pigs. Our results demonstrate the utility of a spatio-temporal examination to inform strategies for limiting the spread of invasive wild pigs.

**Key-words:** feral swine, invasion, invasive wild pigs, range expansion, spatio-temporal model, *Sus scrofa*, wild boar, wildlife damage management

## Introduction

A host of negative ecological impacts from invasive species establish the need to avoid introductions and better predict invasion risk (Fletcher *et al*. 2016). Despite this, reductions in biogeographic barriers continue to promote the global spread of many destructive invasive species (Hobbs 2000), and often the drivers of their spread are not understood (Wilson *et al*. 2009). Identifying influences and constraints of biological invasions and predicting range expansion are crucial for managing detrimental invasive species (Clout & Veitch 2002; Hulme 2003; Hulme *et al*. 2008) and developing anti-invasion policies (e.g., Perrings *et al*. 2005; Lodge *et al*. 2006; Fletcher *et al*. 2016). However, staying ahead of invasions while considering changes in environmental and anthropomorphic conditions is extremely difficult (e.g., Hellmann *et al*. 2008).

Biological invaders exhibit three primary characteristics: rapid spread into novel areas, competitive advantage over existing species and establishment of a dominant population (Valéry *et al*. 2008). One such invader meeting all

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criteria, the invasive wild pig (IWP) *Sus scrofa*, Linnaeus 1758, also referred to as feral hogs, feral pigs, feral swine or wild boar (Keiter, Mayer & Beasley 2016), has been expanding globally following numerous human introductions (Lowe *et al.* 2000). IWPs are the descendants of introduced wild boar, free-ranging/feral domestic pigs and hybrids between these two forms (Keiter, Mayer & Beasley 2016). IWPs have been introduced to all continents except Antarctica, and currently are one of the most widely distributed mammals (Barrios-Garcia & Ballari 2012). The success of IWPs can be largely attributed to their fecund and adaptable biology and generalist feeding behaviour. In addition, populations of IWPs can withstand high mortalities from natural predators and hunters (e.g., Nores, Llaneza & Álvarez 2008; Toïgo *et al.* 2008).

Invasive wild pigs are expanding across large regions of the USA and appear to be gaining momentum (Mayer & Brisbin 2009; Bevins *et al.* 2014; Mayer 2014). IWPs were introduced to the southern USA (e.g., Florida and Texas) by Spanish explorers in the early 1500s (Mayer & Brisbin 2008), but their spread into other regions of the USA was considered mostly negligible until the late 20th century (Waithman *et al.* 1999). Since 2004, a drastic northward expansion has been occurring (Bevins *et al.* 2014). In addition, IWPs began spreading throughout regions of Canada in the late 1980s (Brook & van Beest 2014; Stolle *et al.* 2015) and are threatening expansion into the USA from the north.

Expansion of IWPs into currently unoccupied portions of the USA will escalate the devastating ecological and economic consequences in their nonnative range (Pimentel *et al.* 2000; Seward *et al.* 2004; Barrios-Garcia & Ballari 2012; Bevins *et al.* 2014). IWPs survive on nearly anything edible, including many grasses, forbs and hard mast items (e.g., acorns, etc.) that native wildlife depends upon (Ditchkoff & Mayer 2009). Similarly, IWPs intensely consume agricultural plants (Schley & Roper 2003; Ditchkoff & Mayer 2009), already costing an estimated annual \$1·5 billion (US Dollars) in crop damages and control costs in the USA (Pimentel 2007). In addition, IWPs disrupt ecosystem function and destroy habitat through rooting disturbance, transmission of diseases to livestock and humans and predation on native wildlife (Barrios-Garcia & Ballari 2012; Bevins *et al.* 2014).

Despite a good understanding of the current distribution of IWPs, little information exists to predict when and where they are most likely to spread next. McClure *et al.* (2015) reported that IWPs in the USA were predominantly associated with warm and wet regions, however this was likely attributable to proximity of the original, southern introduction. During the last three decades, populations of IWPs have spread throughout most directional extremes of the continental USA (Southeastern Cooperative Wildlife Disease Study 2015), and currently exist in surrounding Canada (e.g., Brook & van Beest 2014) and Mexico (e.g., Weber 1995; Villarreal González *et al.* 2010). This spread is aided by their rapid population growth, limited natural predation, and ability to quickly adapt to new and suitable conditions (Mayer & Brisbin 2009; Bevins *et al.* 2014). Furthermore, the abilities of IWPs to spread may be enhanced by global changes through time. For instance, conditions in climate and landscape may become more suitable in some regions as they warm from climate change (e.g., Vetter *et al.* 2015), but these relationships are unclear.

Additional uncertainty regarding the spread of IWPs comes from their intertwined natural and anthropogenic-assisted expansion (Bevins *et al.* 2014). Natural expansion occurs when IWPs move into adjacent regions that were unoccupied, possibly because adjacent environments become more suitable or were previously unrealized (e.g., Crooks *et al.* 1999). Anthropogenic-assisted expansion, (i.e., human-seeding), relies on the intentional or unintentional transport and release by humans (e.g., Hulme *et al.* 2008) and is illegal in the USA. The ongoing spread of IWPs has been attributed to unintentional and intentional releases from farms and hunting preserves or enclosures (Mayer & Brisbin 2009; Bevins *et al.* 2014; McCann *et al.* 2014) and intentional transport and release to create recreational hunting opportunities (e.g., Waithman *et al.* 1999; Zivin, Hueth & Zilberman 2000), as well as natural expansion into suitable environments (e.g., McClure *et al.* 2015). However, no forecasts showing where populations of IWPs will become established next have been developed.

A better understanding of the factors influencing the spread of IWPs is needed to predict future expansion and develop anti-invasion strategies. Our objectives were to: (i) determine the environmental characteristics associated with the spread of IWPs into unoccupied areas relative to where they already inhabited, (ii) identify trends in the influences of those environmental characteristics through time and (iii) use this information to predict where IWPs are likely to expand next. To meet these objectives, we developed a dynamic, spatio-temporal model to examine the influences of environmental conditions on the spread of IWPs during three decades of expansion throughout the continental USA. Specifically, we examined characteristics of landscape, climate, human presence, biodiversity and changes in these predictors through time for influences on spread of IWPs across four periods during 1982–2012.

## Materials and methods

### INVASIVE WILD PIG DISTRIBUTION DATA

Distribution data for IWPs throughout the continental USA were obtained from the Southeastern Cooperative Wildlife Disease Study and United States Department of Agriculture Animal Plant and Health Inspection Service (USDA-APHIS) National Feral Swine Damage Management Program, National Feral Swine Mapping System (Southeastern Cooperative Wildlife Disease Study 2015). The data set consisted of spatially explicit polygons describing the known geographic extent of established IWP populations since 1982. Populations were considered established within a county if they were present for ≥2 years with evidence of reproduction (i.e., offspring or mating observed). Data collection was mostly opportunistic with occurrences reported nationally from state wildlife professionals and the USDA via manual drawing of the distributed ranges using a Geographic Information System. As noted by McClure *et al.* (2015), these data were not conducive to typical methodologies that estimate occurrence, colonization or extinction (i.e., comparing occupied vs. unoccupied areas) because the data were not collected in complete presence–absence format. Instead, we structured these data into a unique presence-only approach that took advantage of the temporal construction of the data set by comparing the presences of IWPs between time periods to examine their spread relative to their initial distribution.

We structured the distributional data as follows. We obtained distribution data for 5 years: 1982, 1988, 2004, 2009 and 2012 and aggregated these data to the county level because this was the coarsest spatial grain of data collection throughout the data set. We excluded two counties that were islands (i.e., Nantucket County, MA and San Juan County, WA). We combined the five distributional time steps into four time periods depicting range expansion based on the availability of distributional data: 1982–1988, 1988–2004, 2004–2009 and 2009–2012. For each period, counties occupied by IWPs at the beginning of the time period were designated as *initial range* and denoted as 0, while counties reported to be newly occupied by IWPs by the end of the time period were designated as *expanded range* and denoted as 1 (Fig. 1). Denoting the different ranges this way allowed for modelling the probability of spread (i.e., range expansion) relative to where the IWPs previously inhabited. Extinctions from counties were included by updating the initial range at the beginning of each time period. All other counties not designated as initial or expanded range were excluded from the data set respective to each time period.

## PREDICTOR COVARIATES

### Landscape

For landscape analysis, we used the National Land Cover Database (NLCD) derived from the Landsat Thematic Mapper satellite data (Homer *et al.* 2004). The NLCD is available for four time periods (i.e., 1992, 2001, 2006 and 2011), though direct comparison of NLCD 1992 and subsequent years is confounded by the developments in mapping methodology, new sources of input data and changes in the mapping legend. Thus, we used the NLCD 1992/2001 Retrofit Land Cover Change Product, hereafter NLCD 1992 Retrofit (Fry *et al.* 2009), for the analysis of land cover in 1992. We used a Geographic Information System, (ArcGIS v10.2, Redlands, CA) to consolidate the following land-cover classes in the NLCD 2001, NLCD 2006 and NLCD 2011: open water and perennial ice and snow classes into one class of water/ice; open space developed, low intensity developed, medium intensity developed and high intensity developed into one class of developed land; cultivated crops and pasture/hay into one class of agriculture; deciduous forest, evergreen forest and mixed forest into one class of forest; and woody wetland and emergent herbaceous wetland into one class of wetland. Consolidation of these land-cover types allowed for direct comparison among all NLCDs. Each time period was associated with the NLCD that most closely aligned through time, such that 1982–1988, 1988–2004, 2004–2009 and 2009–2012 were represented by NLCD 1992 Retrofit, NLCD 2001, NLCD 2006 and NLCD 2011, respectively.

For each time period, we extracted landscape composition and configuration predictors that represented important landscape characteristics for IWPs. Agricultural and wetland areas provide important food, shelter and thermal refuge resources for IWPs (Choquenot & Ruscoe 2003; Schley & Roper 2003), while landscape heterogeneity was found to be a key characteristic driving probability of IWP occurrence (McClure *et al.* 2015). Therefore, we used FRAGSTATS v4.1 (McGarigal, Cushman & Ene 2012) and the Geospatial Modelling Environment (GME v0.7.3.0, http://www.spatialecology.com/gme/) to quantify the following land-cover composition predictors within each county: percent of agriculture, percent of wetland and percent of development. We also quantified land-cover configuration predictors for each county: contagion, interspersion–juxtaposition index, edge density and Simpson's Diversity Index of land covers as proxies for landscape heterogeneity. Contagion served as an index of the aggregation and interspersion among all land-cover and land-use patches on a 0–100 scale, where lower values represented highly fragmented and intermixed landscapes. The interspersion–juxtaposition index was a measure of complexity of the landscape on a 0–100 scale, where higher values represented high interspersion of patches. Edge density was a measure of the length of edges between land-cover and land-use patches (km $\text{km}^{-2}$). Simpson's Diversity Index of land covers was a measure of probability, where values near 1 represented high probabilities that 2 random points would be located in different land-cover and land-use patches (i.e., high patch richness).

We quantified temporal changes in landscape characteristics to examine whether the spread of IWPs was influenced by changes in composition or configuration of landscape through time. We calculated change in percent of agriculture, change in percent of wetlands and change in contagion using the nonparametric Sen's slope estimator (e.g., Gocic & Trajkovic 2013). This estimator provided a robust method to calculate a linear trend (i.e., slope) between serially correlated time points (Sen 1968) and was an indicator of the magnitude of change in a given covariate across time. We did not calculate change in landscape characteristics for 1982–1988 because of a lack of reliable land-cover information preceding the early 1990s. For the remaining time periods, we calculated landscape change between two NLCDs most closely aligned with the start and end dates of the time period of interest. For example, landscape change for 1988–2004 time period was calculated using NLCD 1992 Retrofit and NLCD 2001.

### Climate

Climate data for each county were derived from interpolated monthly maximum, minimum and mean temperatures and precipitation at a 2·5-arcmin resolution using the Parameter-elevation Regressions on Independent Slopes Model (PRISM) climate mapping system (Daly *et al.* 2002) using ArcGIS v10.2. We examined a variety of climatic conditions by calculating annual, seasonal and climatic extreme predictors during each time period (i.e., 1982–1988, 1988–2004, 2004–2009 and 2009–2012) for each county. Annual predictors included mean annual temperature and mean annual precipitation. Seasonal predictors included mean maximum temperature of the summer months (i.e.,

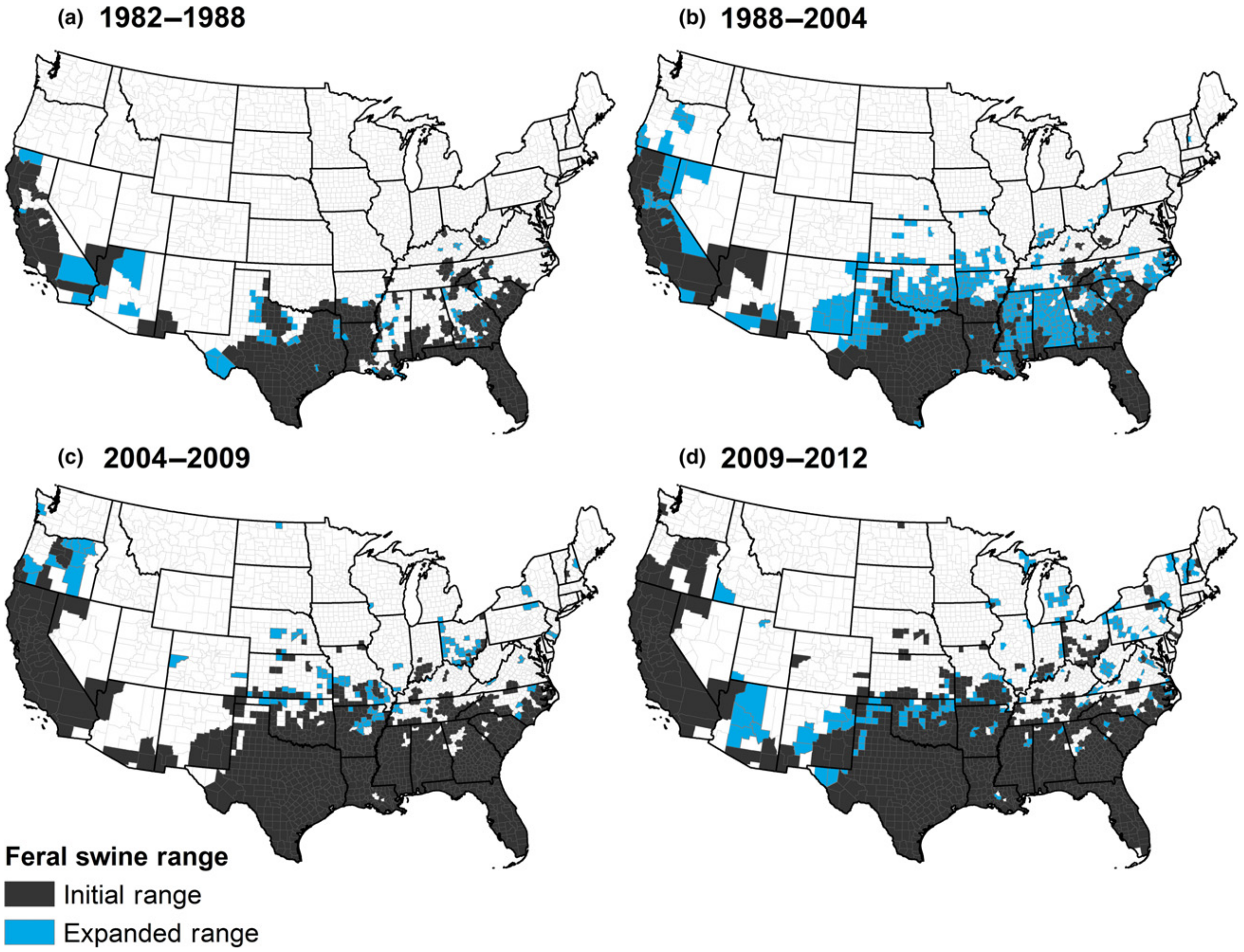

**Fig. 1.** Distribution data showing the spread of invasive wild pigs *Sus scrofa* throughout four time periods in the continental USA. Counties reported to be occupied by invasive wild pigs at the beginning of the each time period were designated as initial range, and any other counties occupied throughout each time period were designated as expanded range. [Colour figure can be viewed at wileyonlinelibrary.com]

June–August), mean minimum temperature of the winter months (i.e., December–February), mean precipitation of the summer months and mean precipitation of the winter months. Climatic extremes predictors included maximum temperature recorded during all years of the time period, minimum temperature recorded during all years of the time period, maximum precipitation recorded during all years of the time period and minimum precipitation recorded during all years of the time period.

To examine the influence of climate change on the spread of IWPs, we quantified temporal trends in climatic characteristics for each time period using Sen's slope estimator. Trend predictors included trend in summer temperature, trend in winter temperature, trend in summer precipitation, trend in winter precipitation, trend in maximum temperature, trend in minimum temperature, trend in maximum precipitation and trend in minimum precipitation.

### *Other predictor covariates*

Distance to water was identified as an important driver of occurrence of IWPs (McClure *et al.* 2015). Therefore, we used the National Hydrography Data set (http://nhd.usgs.gov/data) and ArcGIS to quantify stream density (km $\text{km}^{-2}$; STREAM) for each county. Biodiversity has been suggested as a potential barrier to biological invasion (Kennedy *et al.* 2002); we thus included county-level mammal species richness as an index of biodiversity as one of the predictors. Mammal diversity was obtained from MappingBiodiversity.org (http://biodiversitymapping.org/index.htm) and based on International Union for Conservation of Nature species range maps (Jenkins, Pimm & Joppa 2013). Biodiversity was constant across time periods because time-specific estimates were not available. Lastly, we calculated the average human population density (people per $\text{km}^2$) for each county during each time period based on United States Census data (www.census.gov/data), and trend in human population density under the hypothesis that IWPs are less likely to invade into densely or increasingly densely populated areas.

### RATE OF SPREAD

We calculated the average rate of northward expansion by IWPs throughout the USA. We calculated the Universal Traverse Mercator (UTM) centroid of the IWP distribution during each of the five time steps aggregated to the county level (i.e., 1982, 1988, 2004, 2009 and 2012) using a Geographic Information System. From the centroids, we calculated the rate of expansion per year by subtracting the UTM northing values between time steps.

### STATISTICAL ANALYSIS

We examined the spread of IWPs using a dynamic, spatio-temporal model within a hierarchical Bayesian framework. Advantages of this framework include evaluating all time periods iteratively (e.g., time periods are not independent, and previous time periods inform next time period) while accounting for the proximities of counties to each other (e.g., counties are not independent of adjacent counties). Counties within the continental USA were considered as the spatial units of observation and the four time periods represented the temporal spans of observation. We scaled and centred all predictor variables and conducted an intercorrelation analysis to exclude the predictor(s) in any correlated pair (i.e., $|r| \geq 0{\cdot}60$; Program R v3.2.4; R Development Core Team).

Using our data structured as *initial range* and *expanded range*, we modelled the initial and expanded presence of IWPs per county for each time period, $\boldsymbol{y}_t = (y_{1,t}, \ldots, y_{c,t})'$, where $c = 1, 2, \ldots, N$ counties and $t = 1, 2, 3, 4$ time periods. The response variables were modelled as a function of time period specific regression parameters $\boldsymbol{\beta}_t = (\alpha_t, \beta_1, \ldots, \beta_p)'$ for $p$ predictors, and time period specific spatial random effect parameters $\boldsymbol{w}_t = (w_{1,t}, \ldots, w_{c,t})'$ for each county. The probability of spread of IWPs into a county, relative to where IPWs previously inhabited, was modelled as a Bernoulli random variable, structured as:

$$\boldsymbol{y}_t \sim \mathrm{Bern}(\pi_t) \qquad \text{eqn 1}$$

$$\mathrm{logit}(\pi_t) = \boldsymbol{X}_t \boldsymbol{\beta}_t + \boldsymbol{w}_t \qquad \text{eqn 2}$$

where $\boldsymbol{X}_t$ was comprised of vectors of predictor variable values for time period $t$. We added realistic complexity to the model by incorporating a Markovian time-dependent process (Gelfand, Banerjee & Gamerman 2005; Finley, Banerjee & Gelfand 2012) that allowed for time-varying regression parameters $\boldsymbol{\beta}_t$ such that the prior distributions for $\boldsymbol{\beta}_t$ were updated by the posterior distributions of $\boldsymbol{\beta}_{t-1}$. The temporal structure followed:

$$\boldsymbol{\beta}_t \sim N\left(\boldsymbol{\beta}_{t-1}, \tau_t^2 \boldsymbol{I}\right) \qquad \text{eqn 3}$$

$$\boldsymbol{\beta}_{t=0} \sim N\left(\mu_{\boldsymbol{\beta}}, \tau_0^2 \boldsymbol{I}\right) \qquad \text{eqn 4}$$

$$\tau_t^2 \sim \mathrm{Gamma}(10, 1) \qquad \text{eqn 5}$$

with the hyperpriors $\mu_\beta \sim N(0, 0{\cdot}001)$ and $\tau_0^2 \sim \mathrm{Gamma}(10, 1)$ for precision. The spatial random effects were calculated using Conditional Auto-Regressive priors (Besag, York & Mollié 1991; Gelfand & Vounatsou 2003) with car.normal in GeoBUGS (Thomas *et al.* 2004) to account for the proximities of adjacent counties. The spatial random effects were also constructed to follow a dynamic temporal structure:

$$w_{c,t} = \sum_{N} (\boldsymbol{A} * \boldsymbol{y}_{t-1}) + \eta_{c,t} \qquad \text{eqn 6}$$

$$\eta_{c,t} \sim N(\eta_{c,t-1}, \tau_t^2) \qquad \text{eqn 7}$$

where $\boldsymbol{A}$ was a $N \times N$ adjacency matrix, $\eta_{c,t}$ was the random spatial error and $\tau_t^2 \sim \mathrm{Gamma}(10, 1)$ for precision. We completed the prior specifications with $\eta_{c,t=0} \equiv 0$.

We fit three Markov Chain Monte Carlo (MCMC) chains of 25 000 iterations with burn-ins of 10 000 and thinned by 10 iterations using OpenBUGS 1.4.3 software (MRC Biostatistics Unit, http://www.mrc-bsu.cam.ac.uk/software/bugs/) via package R2OpenBUGS (Sturtz, Ligges & Gelman 2005) in Program R (see Appendix S1, Supporting Information). Convergence and summaries of regression coefficients were generated using the coda package (Plummer *et al.* 2006). We examined the median and 95% credible intervals (CIs) from the distributions of the estimated regression coefficients to identify influences from the environmental predictors on the spread of wild pigs. Specifically, we examined for any overlap of zero by the 95% CIs to indicate statistical and biological influence from the predictors on the spread. Nonoverlapping coefficient estimates would indicate that the probability of spread of IWPs was associated with increasing (or decreasing) values of predictor(s) in the expanded range, relative to previously inhabited range. Whereas overlapping coefficient estimates would indicate that predictor values did not differ between the initial and expanded ranges, and therefore IWPs had spread into counties with similar predictor values.

We initially fitted and independently evaluated 10 *a priori* models based on the categories of land cover, change in land cover, mean annual climate, mean winter and summer climate, climate extremes, change in climate, change in climate extremes, human population density, change in human population density and biodiversity (Table 1). From these initial models, we selected specific predictors for inclusion into a final predictive model. The criterion for selection was based on evidence of statistical and biological influence on the spread of IWPs during the two most recent time periods (2004–2009 and 2009–2012). Although the first two time periods were estimated in the initial models, we focused on the two most recent time periods in attempt to develop a final predictive model that provided the most reliable predictions for where IWPs will spread next.

We used the final model to predict the probability of spread for each county during each time period, extrapolated to all counties of the continental USA. The predictive performance was validated during 2009–2012 using out-of-sample prediction by randomly withholding response data from 10% of the counties during that time period and predicting the outcomes for those counties. The observed and predicted outcomes were compared by examining the proportion of withheld data that were accurately predicted by the model.

Lastly, we assessed the potential for the final model to make accurate predictions of where IWPs are likely to invade next. To assess accuracy, we compared the median predicted probabilities from time period $t$ to the reported range of IWPs during the time period $t + 1$. Specifically, we binned the predictive probabilities from time period $t$ into quartiles, and examined the proportion of counties that were invaded during time period $t + 1$ that fit into each quartile. We considered any counties that were newly invaded and had predicted probabilities of $\geq 0{\cdot}50$ as being correctly classified. We conducted this testing only with counties that were newly invaded and not for counties reported without IWPs because we could not differentiate true- and pseudo-absences.

## Results

Overall, we examined $n = 3106$ counties from the continental USA during time periods 1982–1988, 1988–2004, 2004–2009 and 2009–2012, of which 630, 1078, 1180 and 1358 were occupied by populations of IWPs during the final year of each time period, respectively. The average rate of northward expansion varied by time period. The

**Table 1.** Description of 10 spatio-temporal models used to generate a final predictive model of the probability of spread by invasive wild pigs *Sus scrofa* throughout 3106 counties in the continental USA during four time periods (i.e., 1982–1988, 1988–2004, 2004–2009 and 2009–2012)

| Model | Predictor variables |
|---|---|
| Land cover | AG, WET, CONTAG, SIDI, STREAM |
| ΔLand cover | ΔAG, ΔWET, ΔCONTAG, STREAM |
| Annual climate | ANN_TEMP, ANN_PRECIP |
| Seasonal climate | WIN_TEMP, SUM_TEMP, WIN_PRECIP, SUM_PRECIP |
| Extreme climate | MAX_TEMP, MIN_TEMP, MAX_PRECIP, MIN_PRECIP |
| ΔSeasonal climate | ΔWIN_TEMP, ΔSUM_TEMP, ΔWIN_PRECIP, ΔSUM_PRECIP |
| ΔExtreme climate | ΔMAX_TEMP, ΔMIN_TEMP, ΔMAX_PRECIP, ΔMIN_PRECIP |
| Human | HUM_DENS |
| ΔHuman | ΔHUM_DENS |
| Biodiversity | BIODIV |
| Final | AG, WIN_TEMP, MAX_TEMP, MAX_PRECIP, ΔSUM_TEMP, ΔWIN_PRECIP, BIODIV |

AG, percent agriculture; WET, percent wetlands; CONTAG, contagion (i.e., index of fragmentation); SIDI, Simpson's Diversity Index of land covers; STREAM, stream density (km km$^{-2}$); ANN_TEMP, annual average temperature (°C); ANN_PRECIP, annual average precipitation (mm); WIN_TEMP, annual average winter temperature (°C); SUM_TEMP, annual average summer temperature (°C); WIN_PRECIP, annual average winter precipitation (mm); SUM_PRECIP, annual average summer precipitation (mm); MAX_TEMP, average maximum temperature (°C); MIN_TEMP, average minimum temperature (°C); MAX_PRECIP, average maximum precipitation (mm); MIN_PRECIP, average minimum precipitation (mm); HUM_DENS, annual human density (people per km$^2$); BIODIV, mammalian species richness (i.e., index of biodiversity).

Δ signifies an examination of trend (i.e., slopes) in predictor variables within each time period.

northward rates were 6·5 km year$^{-1}$ during 1982–1988, 7·0 km year$^{-1}$ during 1988–2004, 15·4 km year$^{-1}$ during 2004–2009 and 12·6 km year$^{-1}$ during 2009–2012. The overall northward rate during 1982–2012 was 8·9 km year$^{-1}$.

We found that the measures of interspersion–juxtaposition index and edge density were correlated with contagion, and percent of development was correlated with human population density, therefore we excluded interspersion–juxtaposition index, edge density and percent of development from analysis. Results from the initial models indicated that seven predictors warranted inclusion into the final predictive model: percent of agriculture, winter temperature, maximum temperature, maximum precipitation, trend in summer temperature, trend in winter temperature and biodiversity (see Table S1).

Relative to where IWPs already occurred, results from the final model indicated that spread of IWPs was most strongly associated with the climatic predictor, winter temperature, during all time periods (Fig. 2). The negative association indicated that IWPs were continually spreading into areas with colder winter temperatures. The spread of IWPs was also positively associated with percent of agriculture during two of the four time periods, indicating that IWPs were moving into areas with more agriculture. Other associations showed that IWPs spread into areas with decreasing summer temperatures during 2004–2009, and areas with lower maximum precipitation and decreasing winter precipitation during 2009–2012. Otherwise, IWPs spread into areas containing similar characteristics of temperature, precipitation and biodiversity compared to where they previously inhabited.

Validation of the final model by withholding data was conducted with 135 counties, of which the model correctly predicted 122 (90·3%). For the remaining 13 counties, the model incorrectly classified new invasions as previously occupied counties. The capability of the model to accurately predict the future spread of IWPs varied among the time periods (Fig. 3). Future predictions using shorter time periods (i.e., 1982–1988 for predicting 2004, and 2004–2009 for predicting 2012) were most accurate. Overall, 71% of counties reported with IWPs during 2004 were predicted to have ≥0·50 probability of being invaded, 47% in 2009, and 86% in 2012.

Predictive probabilities from the final model showed that probabilities of spread by IWPs were dynamic through time and increasing, and largely indicative of a northward and westward expansion across the USA (Fig. 4). The probabilities of spread by IWPs were highest in counties adjacent to the 2012 distribution, and decreased farther away from those counties. Prediction from the last time period indicated that the risk of spreading into previously unoccupied counties was highest throughout large portions of western Appalachia (i.e., Tennessee, Kentucky and Ohio), the Midwest (i.e., Kansas, Nebraska, Missouri, Iowa, Illinois and Indiana) and the West and Northwest (i.e., Nevada, Oregon and Washington) regions of the USA. Interestingly, we found a low probability of predicted spread throughout northern Michigan where populations of wild pigs were recently reported (Fig. 1). Confidence in the predicted probabilities varied through time as IWPs expanded (see Fig. S1). We found increasing uncertainty in predictions throughout the northern and southwestern regions of the USA as more sporadic and isolated invasion events seemed to occur in those regions.

## Discussion

The spread of IWPs was largely associated with expansion into adjacent counties containing similar environmental characteristics relative to where IWPs already existed. The most notable exception was the tendency of IWPs to spread into areas with colder winters, a phenomenon that is reflective of their northward expansion from their historically southern distribution in the USA (McClure *et al.*

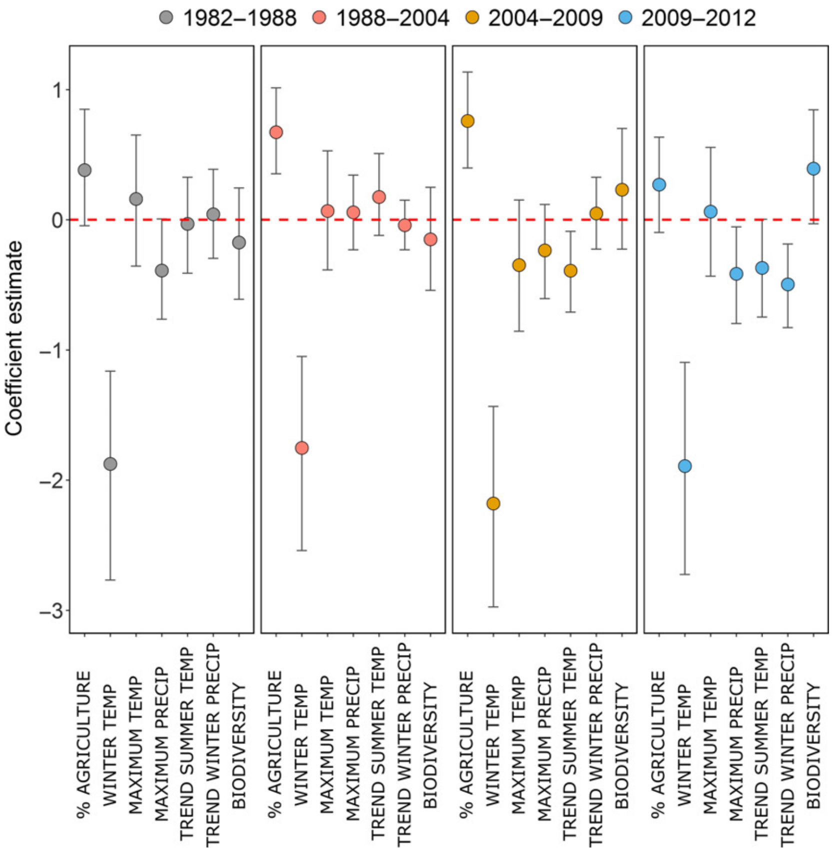

**Fig. 2.** Time-varying regression coefficients (i.e., median values of the posterior distributions) and associated 95% credible intervals for predicting the probability of invasive wild pigs *Sus scrofa* spreading throughout four time periods in the continental USA. Predictor variables are as follows: percent agriculture (% AGRICULTURE), average winter temperature (WINTER TEMP), average maximum temperature (MAXIMUM TEMP), average maximum precipitation (MAXIMUM PRECIP), trend in average summer temperature (TREND SUMMER TEMP), trend in average winter precipitation (TREND WINTER PRECIP) and mammalian species richness (BIODIVERSITY). [Colour figure can be viewed at wileyonlinelibrary.com]

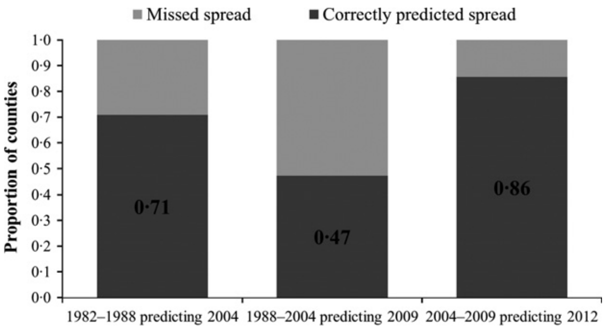

**Fig. 3.** Accuracy assessment of a dynamic, spatio-temporal model for future predictions of invasive wild pigs (IWPs) *Sus scrofa* spreading throughout the continental USA. Median predicted probabilities of ≥0·50 were considered as correctly predicting the spread into a county where IWPs were newly reported. Whereas median predicted probabilities of <0·50 were considered as missing the spread into a county where IWPs were newly reported.

2015). No other obvious trends were identified, although characteristics related to agriculture, summer temperatures and winter precipitation were periodically associated with the spread. A lack of consistent trends coupled with the continued expansion of IWPs indicates that their spread is not reliant on any particular environmental characteristics, and therefore provides little assurance that the spread will cease. This is not surprising considering the range of environmental conditions occupied by wild pigs throughout their circumglobal distribution (Ballari & Barrios-García 2014). Based on the current trajectory of spread (i.e., 12·6 km year$^{-1}$), IWPs could spread throughout most unoccupied portions of the continental USA during the next 3–5 decades, but likely faster if a southward expansion from Canada persists.

Expansion throughout the northern regions of the continental USA should be expected given that IWPs are adapted to cold temperatures. In the native range, the subspecies of Central European wild boar (*S. s. scrofa*) persist through cold winters (e.g., Sáez-Royuela & Telleriia 1986). Lineages from this subspecies have been released or escaped from hunting preserves or enclosures in numerous northern counties (e.g., Michigan Department of Natural Resources 2016; New York State Department of Environmental Conservation 2016; North Dakota Game and Fish Department 2016). Similarly, this subspecies was released from meat farms and hunting preserves or enclosures across Manitoba, Saskatchewan, Alberta, and British Columbia, Canada (Brook & van Beest 2014; Stolle *et al.* 2015), and is now threatening invasion into the USA from the north. These instances of human-seeding followed by natural expansion appear to be escalating an otherwise slower invasion into the cold climate regions of the continental USA, especially considering the more gradual invasion during the last 500 years in warmer regions. Densities and population growth rates of IWPs are lower in colder climates (Melis *et al.* 2006; Vetter *et al.* 2015), further suggesting that human-seeding accelerates spread into the harsher cold climate regions.

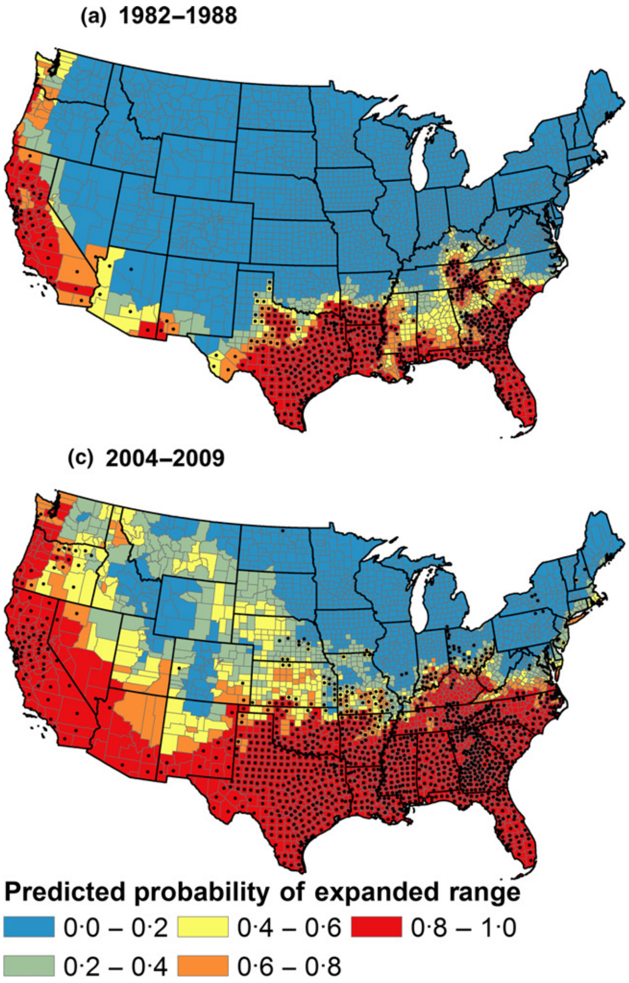

**Fig. 4.** Predicted probabilities generated by a spatio-temporal model of the spread of invasive wild pigs *Sus scrofa* throughout four time periods in the continental USA. Counties in red represent areas that have been, or are highly susceptible to being invaded. Counties in blue represent areas that are least susceptible to spread. Black points indicate the initial and expanded range of *S. scrofa* during each of the four time periods.

As IWPs spread into the northernmost regions of the continental USA, we found some evidence that climate change and precipitation could be facilitating expansion throughout these regions. Areas with declining winter precipitation and lower maximum precipitation had higher probability of spread during 2009–2012. This relationship is characteristic of milder winters, which likely led to the proliferation of Central European wild boar in northern Europe (Sáez-Royuela & Telleriia 1986; Vetter *et al.* 2015). Long periods of snow and ice limit the ability of IWPs to find food while rooting (e.g., Erkinaro *et al.* 1982), thus reductions in snowfall may increase the ability for IWPs to spread. Similarly, milder winters may lead to increased juvenile survival and higher population growth (Vetter *et al.* 2015). Snowfall has been decreasing across much of the continental USA (Kunkel *et al.* 2009). Furthermore, reduction in snowfall could increase hunting opportunities in some areas, and subsequently human-seeding of IWPs for hunting there.

The spread of IWPs was not consistently associated with expansion into more agricultural landscapes, despite extensive use of agriculture where available (Seward *et al.* 2004). During the 1988–2004 and 2004–2009 time periods, IWPs spread into predominantly agricultural areas, portraying their expansion into the agriculturally dominated Midwest. However, this trend diminished during 2009–2012 as IWPs began spreading in agriculture-forest matrix counties of the northern USA. The ability of IWPs to spread regardless of agricultural intensity suggests that agricultural intensity is not a primary determinant of IWP expansion, or perhaps that specific types of crops should be evaluated. However, the Central European wild boar in Europe consumes many types of agricultural crops when available (Schley & Roper 2003; Thurfjell *et al.* 2009), but can also thrive by feeding on nonagricultural plants, animals (i.e., predating and scavenging), and fungi (Ballari & Barrios-García 2014). For this reason, mixed agricultural and forested land covers are preferred because of proximity to food and shelter (Lemel, Truvé & Söderberg 2003; Keuling, Stier & Roth 2009; Thurfjell *et al.* 2009), and also experience higher population growth rates for the subspecies (Bieber & Ruf 2005; Vetter *et al.* 2015).

These types of landscapes are common throughout the Midwest USA where IWPs are spreading.

Model validation indicated the model was capable of accurate predictions, particularly during the shorter time periods. This was likely true because the spread of IWPs is more confined to nearby counties in shorter timeframes, and more widespread and unpredictable during longer timeframes. The most recent time period had the highest accuracy of future predictions, which is most useful for strategic planning. These predictions indicate that western Appalachian, Midwest and Northwest regions of the USA are most immediately susceptible to the spread of IWPs. Overall, these predictions suggest that the spread of IWPs is more imminent than previously suggested (e.g., Waithman *et al.* 1999; McClure *et al.* 2015). We acknowledge that some northern counties might have higher risks than our model demonstrates because of the recent spreading of IWPs in Canada. Interestingly, our predictions and those of McClure *et al.* (2015) both predict that northern Michigan has low probabilities of IWPs despite this region being recently invaded. We expect that isolated human-facilitated movements and unpredictable releases from hunting preserves or enclosures in this region cause this discrepancy, and illustrate the difficult task of predicting human-seeding of IWPs.

After 2004, the probabilities of spread increased dramatically throughout the USA following bursts in reported occurrences of IWP populations. The rate of spread more than doubled during this time, and was likely a consequence of increased human-seeding (Bevins *et al.* 2014). Given that human-seeding of IWPs is highly unpredictable, and IWPs may not be released in areas of high quality habitat, predictions in later time periods were less certain. This uncertainty demonstrates the difficulty of predicting and strategically stopping the spread of IWPs and other invasive species that might be intentionally moved and released by humans. The burst in reported occurrences could also be attributed to increased surveillance after 2004 as the USDA-APHIS began to more intensely examine the spread of IWPs. In addition, using counties as the spatial grain for this analysis exaggerates the distributions of IWPs in some areas, but was necessary based on differences in reporting. Aggregating the IWP distribution data to the county level approximately doubled the area (km$^2$) with reported populations of IWPs during each time period. A consistent and systematic surveillance approach is needed to increase the reliability of future predictions.

## Conclusions

The spread of IWPs in the continental USA exemplifies a global pattern of increasing and aggressive invasive species for which we currently have little understanding about the process of spread (Hobbs 2000). Without immediate and enhanced efforts to curtail the spread of IWPs, we predict that large portions of the USA are in immediate risk of invasion. Spread into these regions will dramatically increase the consequences associated with IWPs such as damage to agriculture and natural resources. Strategies to curtail the spread should focus on coordinated eradication efforts along the boundaries of current distributed areas, and the development and enforcement of anti-invasion policies aimed at stopping human-seeding. The USDA-APHIS National Feral Swine Damage Management Program was created in 2014 with these goals in mind, therefore future evaluations should determine if such a prolific spread can be stopped. Since 2014, success in eliminating and stopping the spread of IWPs has occurred for multiple states (USDA-APHIS, National Feral Swine Damage Management Program, unpublished report) suggesting that stopping the spread is possible with quick responses and improved anti-invasion regulations.

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## Data accessibility

Data used for this study are available at Dryad Digital Repository https://doi.org/10.5061/dryad.22709 (Snow, Jarzyna & VerCauteren 2016).

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## Supporting Information

Details of electronic Supporting Information are provided below.

**Appendix S1.** Spatio-temporal model for examining the spread of invasive wild pigs *Sus scrofa* using OpenBUGS 1.4.3 software (MRC Biostatistics Unit, http://www.mrc-bsu.cam.ac.uk/software/bugs/) via Program R and package R2OpenBUGS.

**Table S1.** Coefficient estimates and their credible intervals resulting from the initial models.

**Fig. S1.** Uncertainty associated with predicted probabilities of spread by invasive wild pigs *Sus scrofa* from a spatio-temporal model displayed as breadth of 95% credible intervals throughout four time periods in the continental USA.