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Original article

Forecasting the range expansion of a recolonising wild boar *Sus scrofa* population

Masayuki Saito, Fumito Koike, Hiroshi Momose, Tosaku Mihira, Seiji Uematsu, Toru Ohtani & Kiichiro Sekiyama

Recolonising native mammals have the potential to cause environmental and agricultural damage. However, if their future distribution can be predicted, effective control measures can be scheduled beforehand to prevent the onset of damage. In this study, we predicted the future range expansion of recolonising wild boar *Sus scrofa* populations in the Chiba Prefecture, Japan, using simulations. Wild boars were extinct in the Chiba Prefecture until the 1970s, but since then, a new naturalised population has spread, probably due to release for hunting. Recently a small, isolated, naturalised population was found in the northern part of the prefecture, which was considered to be a new release. We divided the Chiba Prefecture (5,156 km^2) into 3-km grids and, based on nuisance control records, we examined the 'presence' of wild boar populations from 2002 to 2007 and in 2010. We simultaneously estimated habitat suitability and dispersal probability of the source population via range-expasion modelling. We predicted the future distribution by the use of stochastic simulations for 20 years after 2010. According to the simulations, the wild boar populations will expand into the southern and northern regions of the Chiba Prefecture at a rate of 2,153 km/year, and crop damage should be expected in these areas in the future. Range expansion into the northern region of the prefecture will be completed by around 2025. If the northern isolated population is removed, it will be possible to delay the range expansion for about five years. The eradication of a small isolated population in the northern Chiba Prefecture may have significant economic benefits because the crop production in this area is relatively large.

Key words: dispersal, human-wildlife conflict, range expansion, reintroduction, risk model, Sus scrofa, wild boars

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Recovery of the original range of native mammals is in progress in many industrialised countries. Many large wild mammal species became extinct regionally due to hunting and human settlement during the industrialisation, but they have been recolonising and recovering their geographical ranges since

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the 1990s. For example, the cougar *Puma concolor*, extinct from the mid-western and eastern United States in the early 1900s, is now recolonising these areas (Beier 2009). Sika deer *Cervus nippon*, wild boars *Sus scrofa*, Japanese monkeys *Macaca fuscata* and bears *Ursus arctos* and *U. thibetanus* had disappeared from many regions in Japan, but recently, they have been recovering their native ranges (Tsujino et al. 2010).

Wild boars were extinct in the Chiba Prefecture, Japan, in the 1970s (Chiba Prefecture & Deer Research Group on Boso 2001). Later, probably due to release for hunting, a new naturalised population began to spread. The first wild boar from this new population was captured in 1986, and the number of captures has increased rapidly since then. These newly appearing wild boars are believed to originate from other regions in Japan (Chiba Prefecture & Deer Research Group on Boso 2001). Crop damage by wild boars is also increasing (Chiba Prefecture & Deer Research Group on Boso 2001, Kitazawa & Asada 2010). In 2007, a small, isolated, naturalised population was found in the northern part of the prefecture, where agriculture is economically important, and this was considered to be a new release (Asada 2012).

The geographical range expansion of these recolonising native animals can be predicted using the same methods as those used for controlling alien species (e.g. Lurz et al. 2001, Koike 2006, Fukasawa et al. 2009, Koike & Iwasaki 2011). Observation of the correct population densities and parameters is difficult, and much effort is needed to obtain them (Koike 2006). Therefore, we used simple range-expansion modelling using distribution maps for different years, without population densities and parameters.

Recolonising native mammals often cause damage, such as livestock predation by the cougar and crop damage by wild boars and sika deer. To implement adequate management for reducing damage, the economic contribution of management programmes should be projected at an early stage. Moreover, if their future distribution can be predicted, effective damage control measures can be scheduled beforehand to prevent the onset of damage (Saito et al. 2012). In our study, we estimated the potential habitat suitability and dispersal ability of the wild boar in the Chiba Prefecture, Japan, using the range-expansion modelling developed by Fukasawa et al. (2009). We predicted the future range expansion of wild boars using simulations, and we evaluated the economic outcome of removing the small new population found in 2007.

Material and methods

Study area

Our study was conducted in the Chiba Prefecture (covering 5,156 km^2), Japan (Fig. 1). The climate in the area is classified as warm-temperate with a monthly mean temperature of 4-25°C and a mean annual precipitation of 200-240 cm. Altitudes range from approximately 0 to 408 m a.s.l. Forests cover about 30% of the prefecture. The southern part is hilly and mainly covered by forest. The current vegetation is abandoned deciduous coppice forests of

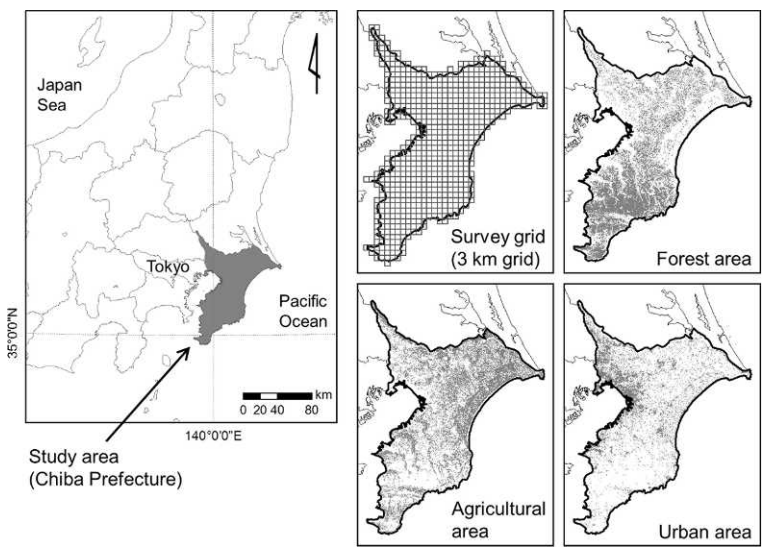


Figure 1. Location and environments of the study area in the Chiba Prefecture, Japan.

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Konara oak *Quercus serrata* and conifer plantations of Japanese cedar *Cryptomeria japonica* (Kabaya 1975). Potential natural vegetation is considered to be evergreen broadleaf forest dominated by evergreen oaks and warm-temperate conifers such as Japanese evergreen oak *Quercus acuta*, bamboo-leafed oak *Quercus myrsinaefolia*, Japanese chinquapin *Castanopsis sieboldii* and Japanese fir *Abies firma* (Miyawaki & Okuda 1976). Agricultural land predominates in the northeastern part of the prefecture, whereas the northwestern part is mainly characterised by suburban residential areas.

Wild boar distribution and environment

We divided the Chiba Prefecture into 3 × 3-km grids (900 ha) as the unit habitat of our metapopulation model (see Fig. 1). The grid size covers the average home range of the wild boar, which is 100-800 ha (100% maximum convex polygon method by Singer et al. 1981, Coblentz & Baber 1987, Sweitzer et al. 2000, Sodeikat & Pohlmeyer 2003, Keuling et al. 2008).

In the Chiba Prefecture, although existing records of wild boar are poor, there are, however, some years for which nuisance-hunting-location data exist. Nuisance control by hunting has been conducted by local agencies to reduce crop damage by wild boars having caused severe damage to rice paddies and other crops. We used these hunting-location data to analyse the geographical distribution from 2002 to 2007 (Nature Conservation Division, Environmental and Community Affairs Department, Chiba Prefecture, Japan, unpubl. data). We also used the hunting locations in 2010 (Nature Conservation Division, Environmental and Community Affairs Department, Chiba Prefecture, Japan, unpubl. data) for model validation and as the initial state of simulation. We treated the 3-km grids with nuisance-hunting-location data as 'presence'-grids of the wild boar population (Fig. 2). Because the sizes of 3-km grids (900 ha) are sufficiently large to evaluate wild boar movement, we could also cover existing areas without crop damage. The distribution of areas with low wild boar densities and no crop damage may be wider than the detected range because nuisance control has not yet been conducted. Consequently, our analysis predicts the range expansion of the high or intermediate density front and is thus suitable for damage prediction.

We used a vegetation map (Ministry of the Environment 1999) to evaluate boar habitat. We obtained data on percentage of forest area, agricultural area and urban area in each 3-km grid. To avoid multicollinearity, we conducted a principal component analysis (PCA) based on these variables. In a preliminary PCA, a larger value of principal component 1 (PC1) represented a high forest cover (Table 1); a larger value of principal component 2

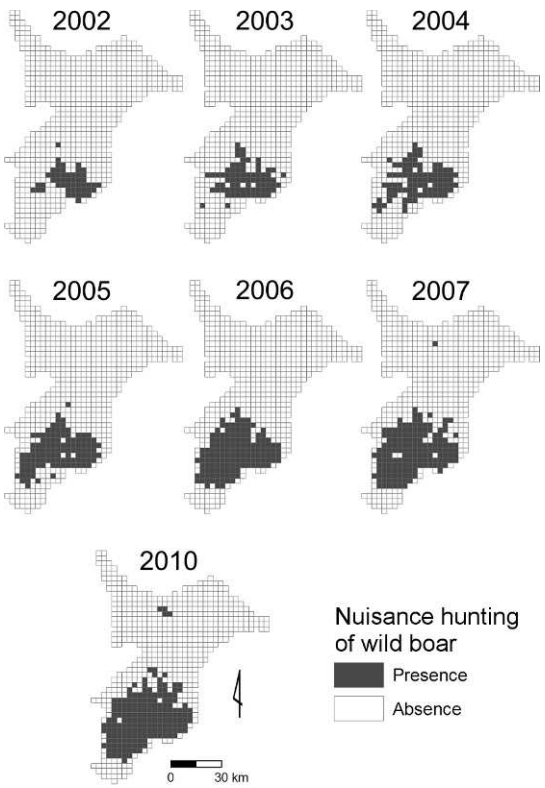


Figure 2. Distribution maps used for range-expansion modelling and the simulation of nuisance-hunting of wild boar in the Chiba Prefecture, Japan. The 3-km grid with nuisance-hunting location data was defined as a 'presence' grid in each of the years of 2002-2010. The new isolated 2007 population in the northern part of the area was excluded from the parameter estimation of the modelling.

Table 1. Preliminary principal component analysis (PCA) for modelling. In the range-expansion modelling, we used principle component 1 (PC1) and principle component 2 (PC2) as environmental variables.

	Loadings	
Land use variable	PC1	PC2
Forest area in %	0.832	-0.019
Agricultural area in %	-0.361	-0.778
Urban area in %	-0.421	0.628
Cumulative proportion	0.58	0.96

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(PC2) was related to urban landscape, whereas a lower value of PC2 was related to agricultural landscape (see Table 1). Thus, we used the scores of PC1 and PC2 from the results of the PCA as environmental variables. We evaluated the product of percent of forest and agricultural areas as an indicator of the forest/agriculture ecotone. This product will be large if the area is an even mixture of forest and agricultural areas. As an indicator of urban areas, we estimated the human population density (i.e. people/km^2) on the basis of 2005 census data (Ministry of Internal Affairs and Communications 2010). We conducted these analyses using ArcInfo 9.3 and the 'princomp' function of the 'stats' package in R 2.11.0 (R Development Core Team 2010).

Range-expansion model

When wild boars are expanding their range, an empty grid will be occupied only if two conditions are satisfied. First, the habitat must be suitable for wild boars; second, the wild boar population must arrive at the focal grid from the source population (Fukasawa et al. 2009). Thus, the probability that wild boars will occur in a given grid (Z_i) is the product of two probabilities: the probability that wild boars can inhabit the grid's environment (habitat suitability, p_i) and the probability that the founder wild boars will arrive at the site during one time step (the probability of dispersal, q_i):

$$Z_i = p_i \times q_i \quad (1).$$

The potential habitat suitability (p_i) is determined by the land use within the focal grid. To describe this factor, we assumed the logistic function that is often used as resource selection probability function (RSPF) with good fitness (Lele & Keim 2006, Keim et al. 2011):

$$p_i = \frac{1}{1 + \exp(-(\alpha_0 + \sum_j \alpha_j X_{ij}))} \quad (2),$$

where α_j is the regression coefficient, X_{ij} represents the jth environmental variable (j = 1 for PC1, j = 2 for PC2, j = 3 for the product of percent of forest and agricultural areas, j = 4 for human population density) at grid i.

We assumed that the dispersal probability (q_i) is determined by the distance from the nearest grid already occupied by a wild boar population (i.e. the source grid). The closer an empty focal grid is to the source grid, the greater the immigration probability. Thus, we used an exponential function:

$$q_i = \exp(\beta D_i) \quad (3),$$

where D_i is the distance from the nearest source grid to the focal grid i, and β is a regression parameter that determines the shape of the exponential kernel. We used the centre-to-centre distance to calculate the distance between two grids. If the focal grid was already occupied by wild boars, D_i is considered to be zero and q_i becomes unity. Because equation (3) did not assume new artificial release, we excluded a grid in the northern part of the prefecture, where wild boars were naturalised in 2007 probably by a new release (see Fig. 2), from the parameterisation.

We fitted the model using maximum-likelihood estimation with the Newton-type non-linear minimisation function 'nlm' in R 2.11.0 (R Development Core Team 2010). In variable selection, we performed a best model selection procedure based on Akaike's information criterion (AIC). We iterated this model selection procedure 2,000 times using a randomly resampled data set (bootstrapping target grid), and obtained a set of 2,000 optimised parameters. We obtained the 95% confidence interval of parameters using this bootstrap method.

Range-expansion simulation and model validation

We predicted the future distribution by simulations using the best range-expansion model. We calculated the probability that a wild boar population was present in each grid using equation (1) and determined the 'presence' or 'absence' stochastically, using a random number. Since one simulation gives either 'presence' or 'absence', we iterated this simulation 500 times to calculate the incidence probability for each grid. In order to evaluate the uncertainty of parameters, we iterated all of the simulations 500 times. In these simulations, we randomly selected a parameter set from 2,000 sets of parameters obtained by the above 2,000-iteration bootstrap method. We used a given parameter set throughout the simulations to determine incidence probability. We determined the median and interquartile points (25th and 75th percentile) of the incidence probability. A small interquartile range indicates a reliable prediction.

To validate the best range-expansion model, we evaluated the accuracy of the simulation by the area under the receiver operating characteristic curve (AUC), the correct classification rate (CCR) between observed values in 2010 (see Fig. 2) and the predicted

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Table 2. Parameter estimate of the best range-expansion model based on model selection. Environmental variables were standardised. The 95% confidence interval of each variable is based on a 2,000-iteration bootstrap resampling.

Variable	Coefficient	95% confidence interval	
		2.5% point	97.5% point
(Intercept)	0.773	0.314	1.281
PC1	1.615	0.837	1.539
PC2	-		
Forest area in % × Agricultural area in %	0.86	0.491	1.268
Human population density (people/km^2)	-		
Distance from the nearest presence grid in the last year (in m)	-3.218×10^{-4}	-3.587×10^{-4}	-2.892×10^{-4}

values (median incidence probability) in 2010 after the distribution in 2007. The AUC evaluates how well model predictions discriminate between locations where observations are present and absent, and it is one of the most widely used threshold-independent evaluators of model discriminatory power (Fielding & Bell 1997). We adjusted the cut-off point for determining the CCR to minimise the difference between sensitivity and specificity.

In the simulation of future distributions, we prepared two scenarios: the range expansion from the whole geographical distribution in 2010 (scenario #1) and the range expansion excluding the new northern population found in 2007 by removing this population (scenario #2).

Evaluation of eradication programme

To evaluate the economic advantage of removing the small new population found in 2007, we compared the predicted crop damage between scenario #1 and scenario #2. We then estimated the potential amount of money lost from crop damage in 37 municipalities of the northern part of the area not having a wild boar population. In accordance with Asada (2011), we estimated the potential damage amount, which is the product of the total amount of agricultural production within 10 m of the forest edges in each municipality, and the damage rate (0.1) applicable to each municipality. Based on the observed data in the six southern municipalities, the damage rate of 0.1 was calculated from the damage amount in 2009, and the amount of agricultural production within 10 m of the forest edges (Asada 2011). If the municipality overlapped the centre point of the grid, the median incidence probability was $\geq$ 50%, and we assumed that wild boar damage would be occurring in that municipality. We estimated the cumulative amount of money lost by crop damage from 2011 to 2030 in each scenario. The difference in values between scenarios #1 and #2 indicates the economic advantage of the eradication programme.

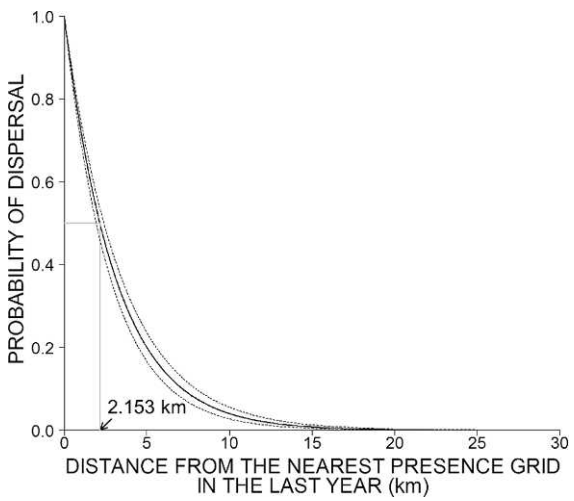


Figure 3. Estimated dispersal kernel in the Chiba Prefecture, Japan. The solid line was drawn using the mean value of the posterior distribution of the coefficient, and the dashed lines using the upper and lower limit of the 95% confidence interval. The grey line indicates the dispersal distance at a probability of 50%.

Results

Wild boars prefer forest and forest/agriculture ecotones. As shown by PC1, the product of percent of forest and agricultural areas is a positive factor in range-expansion modelling (Table 2). The distance from the nearest source grid was significant, and an empty grid close to the population tended to be occupied (see Table 2). By estimated dispersal kernel, if the grid was 2,153 km distant from the occupied grid, an empty grid would be occupied within one year at a probability of 50% (Fig. 3). Our range-expansion model had good accuracy, as confirmed by the AUC of 0.981 and the CCR of 0.929 (Table 3 and Fig. 4).

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Table 3. Classification accuracy between observed values in 2010 and the values predicted for 2010. The predicted values were median incidence probability obtained from the simulation after the distribution in 2007 using the best range-expansion model. Correct classification rate (CCR) was 0.929. The cut-off point for determining the CCR was adjusted to minimise the difference between sensitivity and specificity.

	Observed		
	Presence	Absence	Total
Predicted			
Presence	171	36	207
Absence	13	469	482
Total	184	505	689

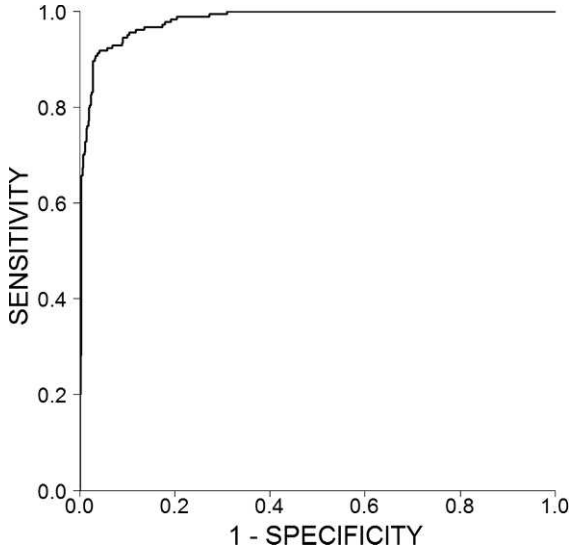


Figure 4. Receiver operating characteristic (ROC) curve for the model validation between observed values in 2010 and the predicted values in 2010. The predicted values were median incidence probability obtained from the simulation after the distribution in 2007 using the best range-expansion model. The area under the ROC curve (AUC) was 0.981.

Based on our simulation, wild boars will arrive in the southern part of the prefecture by 2016 (scenario #1). By 2025, they will have spread to the northern part of the prefecture, where forests are scattered in an important agricultural area, although the median incidence probability was low due to unsuitable habitat (lacking sufficient forest; Fig. 5). Wild boars will not spread to the northeastern urban areas. Simulation scenario #2, i.e. removing the isolated

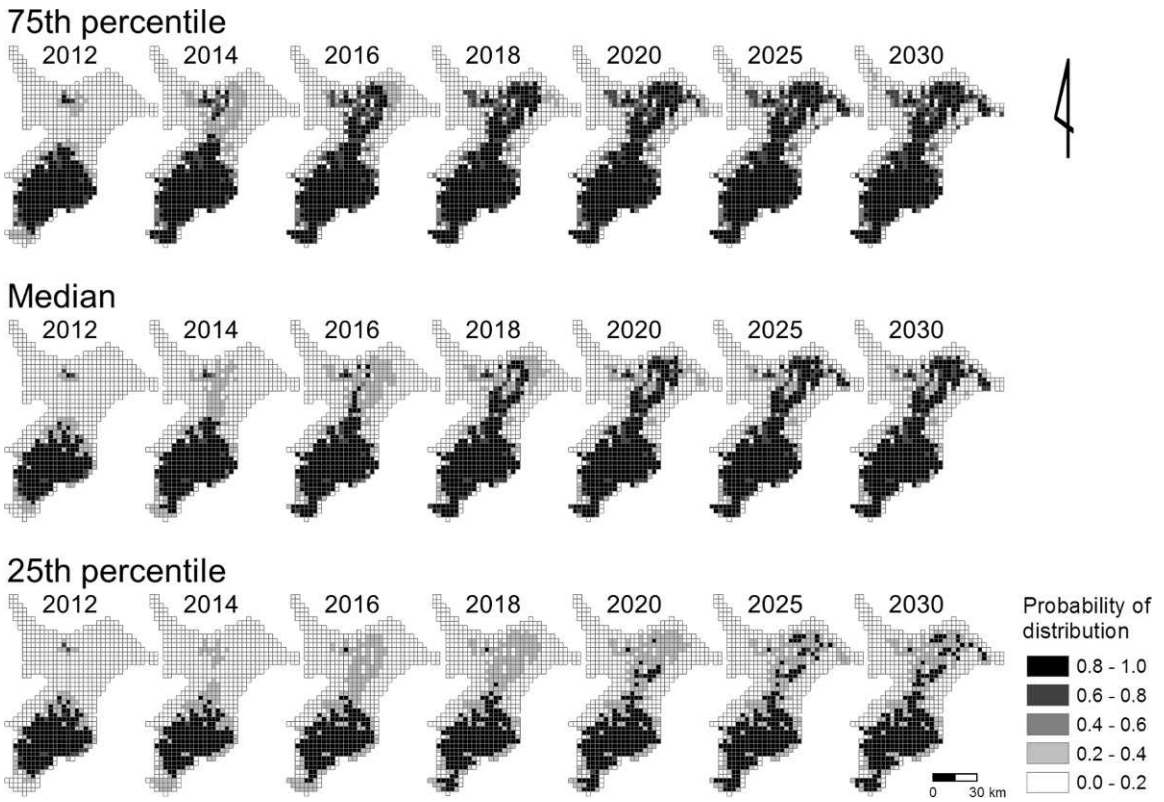


Figure 5. Predicted probability of the distribution of wild boar using simulation scenario #1 in the Chiba Prefecture, Japan. The median and interquartile points (25th and 75th percentiles) of incidence probability in 500 iterated simulations are shown.

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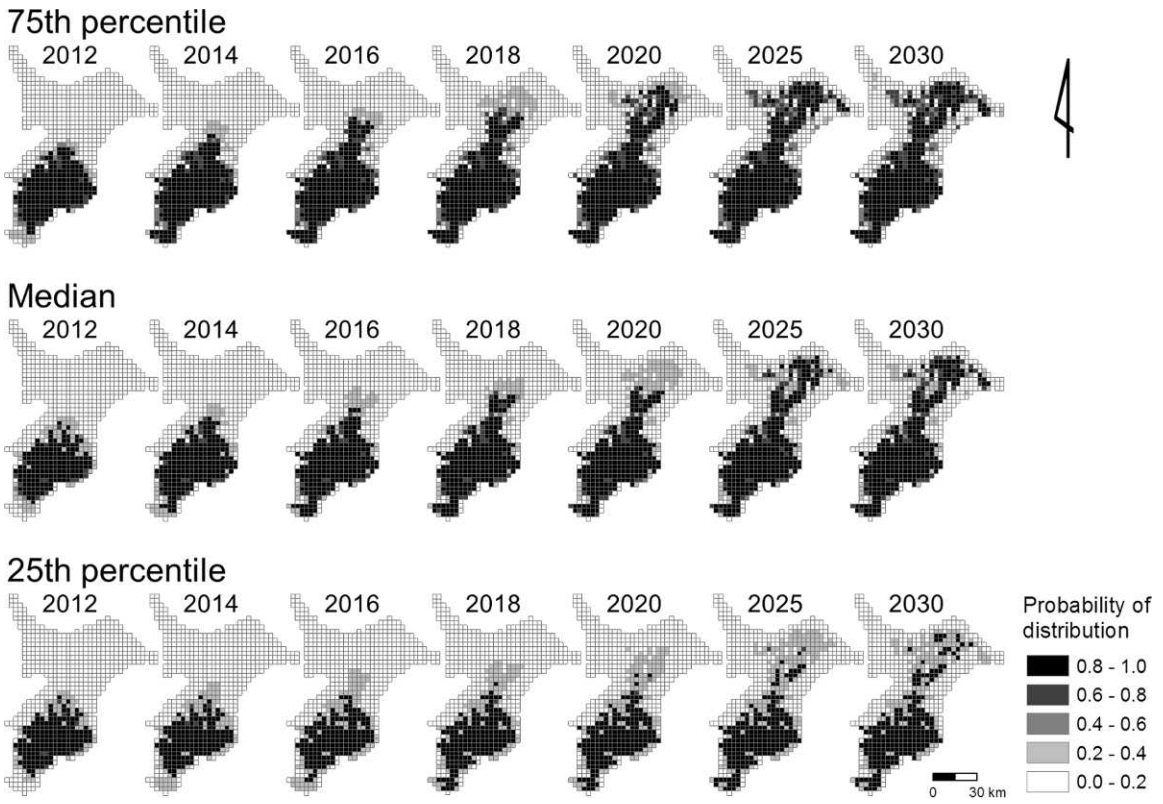


Figure 6. Predicted probability of the distribution of wild boar using simulation scenario #2 in the Chiba Prefecture, Japan. The median and interquartile points (25th and 75th percentiles) of incidence probability in 500 iterated simulations are shown.

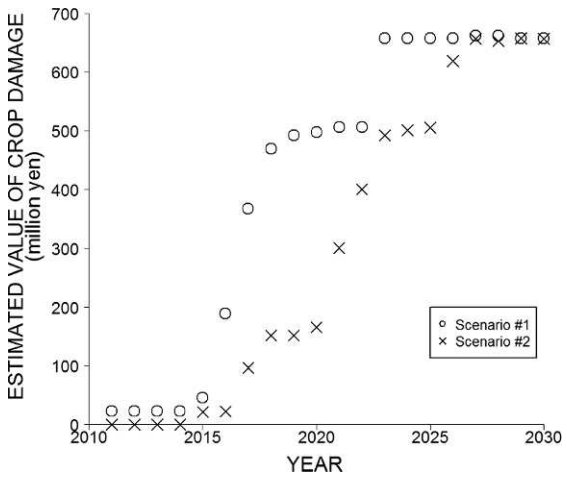


Figure 7. Estimation of the amount of money lost due to wild boar damage in the northern area of the Chiba Prefecture, Japan. The values were calculated on the basis of the amount of agricultural production within 10 m of forest edges in the 37 northern municipalities, and the damage rate (0.1) in the southern six municipalities in 2009 (Asada 2011).

population, showed that range expansion to the northern region of the prefecture would be completed by around 2030 (Fig. 6), five years later than in scenario #1.

After the range expansion was saturated, the uncertainties of the incidence probability in the northern region were higher than in the southern region (see Figs. 5 and 6). This uncertainty represented a high sensitivity of the incidence probability to the fluctuation of estimated parameters in this region. The persistence of wild boar presence in the northern area was highly uncertain especially in grids with less forest and bordering an urban area. Uncertainty was low in urban-core (never inhabited) and inland-forest (definitely inhabited) areas.

The value of crop damage will increase with the range expansion of wild boar populations (Fig. 7). The estimated cumulative value of crop damage from 2011 to 2030 was 8,434 million yen (scenario #1) and 6,052 million yen (scenario #2). This indicates that the economic contribution of the eradication programme would be 2,382 million yen.

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Discussion

We forecast the range expansion of a wild boar population based on distribution maps for different years. Although population densities and parameters were not used, the best model obtained correctly predicted the range expansion (0.981 AUC and 0.929 CCR; see Table 3 and Fig. 4). In the early stage of range expansion of a species, we usually have to predict range expansion based on limited information without population parameters (Koike 2006). Therefore, our simple and reliable range-expansion modelling is helpful in reducing the risk of crop damage.

Our model predicts that the wild boar population in the Chiba Prefecture will expand its range at the rate of 2,153 km/year (see Fig. 3), which is similar to the female dispersal distances of 2-3 km measured in Sweden (Truvé & Lemel 2003) and 1.6 km in Germany (Keuling et al. 2010). In our simulations, wild boar populations will expand to the southern and northern regions of the Chiba Prefecture (see Fig. 5), and crop damage will occur in these areas in future. The northern area of the prefecture produces a range of agricultural products (such as peanuts *Arachis hypogaea*), and damage is likely to become a significant social problem in this area.

If the northern isolated population is removed (scenario #2), it will be possible to delay the range expansion for about five years. We can calculate the economic contribution of this eradication project. The net gain from reducing crop damage by removing the northern population for five years will be 2,382 million yen, whereas the eradication cost for this small population will be 400 million yen (based on the wild pig eradication for 194 km^2 using intensive fencing in Santa Cruz Island, California; Schuyler et al. 2002). In particular, if the northern population is removed by 2015, the reduction in damage will be large (see Fig. 7). This suggests that an eradication programme will have agricultural benefits. A predicted future-range expansion map can then be used to determine the optimal position of fences to avoid further range expansion.

Another effective utilisation of the forecasted range expansion would be to implement preventive measures before the arrival of a wild boar population (Saito et al. 2012). Effective control such as fencing, environmental improvements and reducing population density around cropland can reduce the damage (Eguchi 2008, Honda et al. 2008, Saito et al. 2011). The local government can provide helpful information and present lectures for farmers before the range expansion occurs.

Forest area and the forest/agriculture ecotone are suitable for wild boars (see Table 2). Although agricultural areas are also preferred because they provide food sources (Schley & Roper 2003), larger agricultural areas limit the availability of shelter (Herrero et al. 2006). Urban areas do not provide good habitat for wild boars (see Table 2). Park & Lee (2003) have suggested that wild boars in Korea avoid human contact, but in Berlin, and elsewhere in Germany, wild boars do appear in urban environments (Jansen et al. 2007). It is possible that wild boars on the Boso Peninsula have not yet become habituated to humans. The possibility that boars will adapt to urban environments should be considered carefully.

The distribution data used in our study were obtained from a nuisance-control programme for reducing wild boar damage. Thus, the distribution of low-density wild boar populations that do not cause damage may be wider than the detected range (see Fig. 2). Our simulation predicts the range expansion of a high or intermediate density front and may therefore be suitable for damage prediction.

Our model can be regarded as a risk model based on distribution maps and damage data at the level of the municipality. Because the distribution, environment and damage data used in this study are easy to obtain, our methods could be useful in predicting the risk of damage in other regions that have recently begun to experience damage by wild boars and other animals. Moreover, even if there are no distribution data, it is possible to predict damage risk using presence-only damage data (Saito et al. 2012). By applying various risk models, according to the stage of available information, risk-reduction strategies can be optimised.

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