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ORIGINAL PAPER

Assessing and predicting the spread of non-native raccoons in Germany using hunting bag data and dispersal weighted models

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Abstract As the second largest cause of biodiversity loss worldwide, there is an urgent need to study the dynamics of biological invasions and identify factors limiting the distribution of invasive alien species. In the present study we analyze national-scale hunting bag data from Germany to predict the dispersal of raccoons in the largest non-native population of the species. Our focus is (1) to document changes in the distribution and abundance of raccoons, (2) to identify the species–environment relationship and predict which areas will be suitable for future colonization and (3) to apply a dispersal model to predict how fast the raccoon will spread to these areas. The increase from about 9000 harvested raccoons in 2000/01 to about 71,000 in 2011/12 reflects the extensive amount of suitable habitat for this omnivorous species in Central Europe. The best model for explaining range expansion in Germany identified coverage of agriculture and fragmentation and coverage of forests as the most important explanatory variables. The range of raccoons (area with harvest index >0.1 per 100 ha) increased from 26,515 km^2 in 2001 to 111,630 km^2 in 2011, and is predicted to expand to 252,940 km^2 by 2061, 71 % of the area of Germany. This vast area encompasses strategically important areas for conservation biology, such as wetlands with endangered native terrapins. The combination of merging of separated introduced populations and accelerating population growth

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highlights the potential for future impacts of raccoons on native communities, ecosystems and economic life in Germany and Central Europe.

Keywords Invasive species · Wildlife management · Species–environment relationship · Dispersal weighting · Habitat favorability · Species distribution model

Introduction

Worldwide, invasive alien species (IAS) are associated with significant damage to the economy and public health, and are considered to be one of the major threats to native biodiversity (Mack et al. 2000; Pimentel et al. 2005; Hulme 2007; Pyšek and Richardson 2010; Keller et al. 2011). Hence a major challenge lies in determining factors causing invasion success and predicting the potential distribution of non-native species. Wildlife monitoring programs help to determine the distribution of non-native species, which is necessary in order to assess the impact of non-native species in terms of disease risks, economic damage and negative effects on native species and the environment, and plan management actions to reduce these impacts (Engeman et al. 2006; Sterner and Smith 2006; Yokomizo et al. 2009). Monitoring programs for terrestrial mammals are usually based on the collation of ad-hoc records (Roy et al. 2014a), systematic surveys of abundance (such as road-kill surveys, tracking plots, spotlighting, pellet counts along fixed routes), or more cost intensive and logistically complicated methods such as radio-tracking, mark-recapture, camera trapping, aerial surveys and DNA genotyping (Woodroffe et al. 1990; Bartel et al. 2012; Engeman et al. 2013). Hunting bag data are routinely collected for game species, and these offer an additional monitoring strategy as they can be used as a general index of long term trends, population and distribution change and a proxy of abundance across time (Cattadori et al. 2003; Kitson 2004; Carlsson et al. 2010).

These abundance or presence/absence data are used in species distribution models (SDMs) to identify suitable or unsuitable areas for a species based on a set of environmental covariates, and these SDMs can be used to predict where a non-native species will spread to. Generally SDMs assume that the species being modelled is at equilibrium with the environment (Guisan and Thuiller 2005), which means unoccupied areas are considered as unsuitable for the species. However non-native species are often spreading from a few release sites and are therefore not at equilibrium with their environment, so absences may be due to dispersal limitation as well as unsuitable environmental conditions (Václavík and Meentemeyer 2012). One approach to address this is to model the dispersal process, and then weight the species distribution model by the predicted probability of different areas being dispersed to (Sullivan et al. 2012). This procedure reduces the influence of areas where a species is absent due to dispersal limitation in model fitting, so conforms more closely with the assumptions of SDMs. Approaches that directly model the dispersal process (e.g. Sullivan et al. 2012), or account for spatial autocorrelation introduced by dispersal limitation (Václavík et al. 2012; Thomas and Moloney 2015), potentially allow SDMs to be safely used on spreading non-native species. We apply these methods to analyze raccoon (*Procyon lotor* Linné 1758) hunting bag data from Germany.

Raccoons were introduced in different European countries by deliberate or accidental releases occurring since the early twentieth century (Beltrán-Beck et al. 2012). They have become widely established, and are considered a pest in several places due to the economic damage they cause, their threat to public health and negative interactions (competition and predation) with native species (Ikeda et al. 2004; Beltrán-Beck et al. 2012; Vos et al. 2012, 2013). Additionally, they were identified as one of the top ten invasive alien species with the greatest potential to threaten biodiversity in Great Britain (Roy et al. 2014b). In Europe the largest non-native population is found in Germany, and is commonly assumed to stem from two separate founding events in Central (1934, Edersee) and Northeast Germany (1945, Wolfshagen) (Stubbe 1975; Lutz

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1984). Recent genetic studies (Frantz et al. 2013; Fischer et al. 2015) propose an additional founder population in the federal state Saxony near the Polish border and a further introduction event in the Harz region, which may influence the distribution and abundance of raccoons in Central Europe (see Fig. 1).

Population densities in the native range are usually around 10–12 raccoons per 100 ha (Kaufmann 1982) and can reach 333 individuals per 100 ha in urban sites (Riley et al. 1998). Population densities in the non-native range are lower than this, with the highest densities in swamp areas of Northeastern Germany (Müritz National Park) with 6–8 individuals per 100 ha (Muschik et al. 2011) and in the urban areas of Bad Karlshafen and Kassel in Central Germany where densities exceed 100 individuals per 100 ha (Hohmann and Bartussek 2011). The forested Solling mountains probably provide the most comparable habitat to that typically occupied in the native range, and population densities here are 1–4 individuals per 100 ha (Hohmann 1998). These lower population densities to comparable habitat in the native range indicate the potential for future population growth in Germany.

Although Germany represents the core of the non-native range in Europe, information about the current status of the raccoon and the patterns of range expansion at a national scale is still rare. In this paper we analyze hunting bag data at administrative district level to map the spread of raccoons over an entire country, and correlate this with landscape structure to predict environmental suitability. We predict future trends and discuss the consequences of increasing population size, the merging of separate introduced populations and the potential future distribution.

Approaches like this may provide valuable evidence informing the management of alien species, as hunting bag data are easily obtained over a wide scale of regions and so can be used to assess the extent of colonization, especially for species for which alternative data are rare.

Materials and methods

Hunting bag data as indicator for raccoon relative abundance

Although there are known problems related to the use of hunting statistics as population indexes (Hornell-Willebrand et al. 2006; Ranta et al. 2008), several comparisons of census data and hunting bag statistics suggested largely similar conclusions from both data sources (Baines and Hudson 1995; Cattadori et al. 2003; Imperio et al. 2010 Knauer et al. 2010). Thus to analyze the population dynamics of raccoons in Germany, annual hunting bag data at administrative district level (412 districts, status 2009), gathered up by the German wildlife information system database (WILD), which is commissioned by the German Hunting Association (Deutscher Jagdverband e.V.), were scanned for 12 hunting seasons from 2000/01 to 2011/12 (hunting seasons cover the time from 1 April to 31 March). Hunting season for raccoons in Germany is open all year round except for females nursing young and in the federal states Bremen and Saarland. Recordings include specimens found dead and include both hunting in private and state owned land. The data were calculated relative to the total district areas, which vary from 36 to 3085 km^2, to give the density of records in each district. This allows levels of invasion to be quantified consistently over the study area.

In 2007, 2008 and 2011 three district reforms have taken place in Germany, in the federal districts Saxony-Anhalt, Saxony and Mecklenburg-Western Pomerania respectively. To assure comparable data we allocated the records from the former Saxony-Anhalt and Saxony districts to the new districts, whereas we used the existing borders of Mecklenburg-Western Pomerania from 2010. Where information was available, islands in the German and the Baltic Sea were treated separately to the administrative districts they belonged to, as raccoons have so far been unable to reach them. For hunting seasons from 2002/03 to 2007/08 as well as for the years 2010/11 and 2011/12 no information about the state hunting (1–5 % of the common raccoon bag) records was available for the federal district Thuringia. Furthermore a lack of regional level harvest records existed for Saxony-Anhalt for hunting years 2003/04 and 2004/05. Maps of district boundaries were created in the Geographical Information Systems ArcGIS 10.1 (ESRI Inc, Redlands, CA, USA), using ESRI Data and Maps (2000, 2005) and infas GEOdaten district borders (2009), projected to Transversal Mercator, Potsdam, Bessel.

In order to get a general idea about the raccoon range expansion, hunting bag data were arranged in

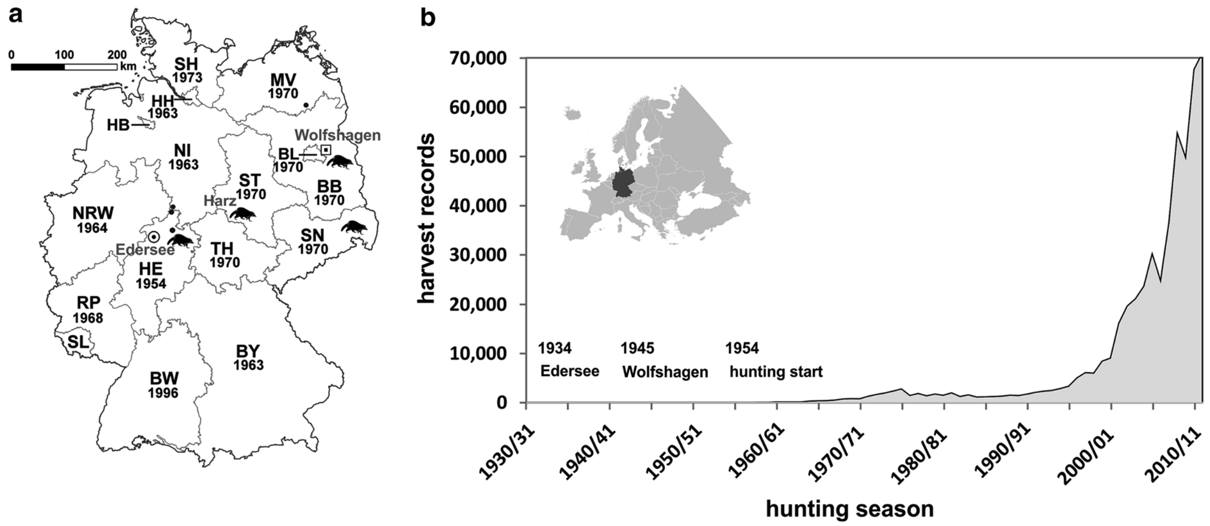

Fig. 1 Starting points, hunting start dates and change in raccoon populations in Germany. **a** *Grey lines* and *bold letters* represent the boundaries and abbreviation of the German federal states respectively: BB, Brandenburg; BL, Berlin; BW, Baden-Württemberg; BY, Bavaria; HB, Bremen; HE, Hesse; HH, Hamburg; MV, Mecklenburg-Western Pomerania; NI, Lower Saxony; NRW, North Rhine-Westphalia; RP, Rhineland-Palatinate; SH, Schleswig–Holstein; SL, Saarland; SN, Saxony; ST, Saxony-Anhalt; TH, Thuringia. The years give information when the raccoon was declared a game species in each federal state (Hohmann and Bartussek 2011). *Edersee* and *Wolfshagen* indicate the geographic locations of the two introduced populations in 1934 and 1945. In the Harz region and SN additional founder population were proposed (Frantz et al. 2013; Fischer et al. 2015). *Black points* represent the location studies revealing raccoon densities, in the urban habitats of Kassel and Bad Karlshafen in HE, in the low mountain forests in Solling in NI and in the swamp areas in Müritz in MV. **b** The collected harvest records suggest an exponential trend in the last decade. Our study covers the strong increase beginning in 2000

the following density classes: (1) absent, 0; (2) very low, 0–0.01; (3) low, 0.01–0.1; (4) medium, 0.1–0.5; (5) high, 0.5–1 and (6) very high, >1 individuals per 100 ha. Sporadic records of single harvested raccoons are likely to relate to transient individuals rather than established populations; we therefore converted all districts with $x < 0.1$ raccoons per 100 ha to absent for the correlation and regression analysis. This approach focuses our analysis onto highly suitable areas that we are confident hold established populations of raccoons, but by potentially excluding some established populations with densities below this threshold our model predictions will be more conservative than if we had classed all districts with raccoon records as occupied.

Explanatory variables of landscape structure

Macrohabitat characteristics of all 412 administrative districts were calculated on the basis of the CORINE Land Cover (CLC2006—100 m) using FRAGSTATS 4.1 (McGarigal et al. 2002). The original land cover information containing 44 classes (37 classes for Germany) was reclassified into the following six habitat classes, representing habitat classes considered potentially suitable for raccoons: artificial (C1), agriculture (C2), pasture and open areas (C3), forests (C4), scrubland (C5) and wetlands and waterbodies (C6) (see Online Resource Table S1). The effect of the environmental structure on the raccoon dispersal was analyzed at vegetation-class level using the districts as sampling units. In order to characterize the habitat structure of the districts, we used the following indices:

- Percentage of landscape (termed PLAND) quantified the proportional amount of each of the six vegetation class types (C1–C6) in the landscape on district level.
- Clumpiness index (termed CLUMPY) provides an effective index of fragmentation of patch types that ranges from −1 when the patch type is maximally disaggregated to 1 when the patch type is maximally clumped.

Calculating dispersal probabilities

The distribution of spreading alien species is influenced by their ability to disperse from existing occupied areas as well as by environmental suitability. We therefore constructed a dispersal model to calculate the probability of districts being dispersed to, where the probability of a district being colonized was modelled as a function of distance (km) from the nearest district occupied in the previous time step. Distances between districts were measured as the Euclidean distance between district centroids on a Transversal Mercator grid. We assume that the probability of a district being dispersed to declines with distance following a negative exponential distribution, so the decline in dispersal probability P with distance is given by $P = \mathrm{e}^{-bx}$, with the parameter b determining the rate of decline, and x denoting distance. We estimated b using maximum likelihood. In order to do this, we first re-wrote the dispersal kernel into a logit scale,

$$\mathrm{logit}(P) = \log(P/1 - P) = \log\left(e^{-bx}/\left(1 - e^{-bx}\right)\right).$$

This was then substituted into a binomial likelihood function,

$$\text{likelihood} = \Sigma - y \cdot \log\left(1 + \mathrm{e}^{P}\right) - \left(\left(1 - y\right) \cdot \left(1 + \mathrm{e}^{P}\right)\right),$$

where P is the dispersal probability calculated from the dispersal kernel and y is the occupancy status of the district. We note that this dispersal model does not explicitly distinguish between neighborhood diffusion and long-distance dispersal (Shigesada et al. 1995), although both processes implicitly contribute towards the estimated dispersal kernel. Additionally, we assume that the dispersal kernel does not vary spatially or in time. Analyses were conducted in R (R Core Team 2012).

Habitat suitability analysis

All land-cover variables for the model were checked for their independence by running a collinearity procedure in IBM SPSS Statistics Version 21 (Pearson correlation $r < 0.7$; variance inflation factor <3) and as a result, the variable PLAND_1 was excluded from the analysis. We applied a logistic binominal generalized linear model (GLM) in R, including the vector of dispersal probabilities as prior weights. This weighting reduces the influence of areas that are unlikely to have been dispersed to, and has been shown to improve the ability of SDMs to characterize the species environment relationship of species that are not at equilibrium with their environment (Sullivan et al. 2012). For the selection of the most parsimonious model we used the stepAIC function from the MASS package (Venables and Ripley 2002) to remove covariates from SDMs in a stepwise fashion based on the Akaike information criterion. Absolute predicted probabilities of occurrence are sensitive to a species' prevalence, so we used the inverse of logit transformation (Real et al. 2006) to calculate the environmental favorability function for or against the species presence.

$$\mathrm{F} = \mathrm{e}^{y}/(\mathrm{n}_1/\mathrm{n}_0 + \mathrm{e}^{y})$$

with $y = \ln(n_1/n_0) + \alpha + \beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_n x_n$, where α is a constant, n_1/n_0 = presence/absence ratio and $\beta_1, \beta_2, \ldots, \beta_n$ are the coefficients of the n predictor variables $x_1, x_2, \ldots, x_n$. We modified the function to account for dispersal weighting by replacing n_1/n_0 by $n_1/(n_0 \cdot \Sigma P)$.

Calibration and validation of models

We modelled the spread of raccoons over two 5 year time steps (2001–2006 and 2006–2011). We divided our data into these time steps, rather than investigate spread between each year, as our district level occurrence data is too coarse to reliably detect movements of a single generation of dispersing raccoons; 85 % of raccoons have been found to disperse <3 km (Cullingham et al. 2008), whereas the median distance between neighboring district centroids is 20.2 km. We therefore assume that movement between districts results from the cumulative movement of multiple generations of raccoons, and that this cumulative movement can be modelled using a dispersal kernel. The choice of time step length was motivated by the desire to have a long enough time period to allow movement between districts while allowing multiple time steps within our study period. The distribution of raccoons at each time point was obtained by pooling records from the two hunting seasons containing the target year (i.e. data for 2001 cover hunting between 1 April 2000 and 31 March 2002). Data were pooled in this way to reduce the effect of any fluctuation in hunting effort between hunting seasons, with the assumption that differences in distribution between adjacent hunting seasons primarily reflects differences in hunting effort, while differences in distribution between time steps primarily reflects genuine changes in distribution.

We used data from the first time step (i.e. spread between 2001 and 2006) to calibrate dispersal models and SDMs, and use these to predict the distribution at the end of the second time-step (using the cellular automata simulation described below run for one time step). This approach allowed us to use independent data to calibrate and validate models predicting the spread of raccoons. We then repeated the modelling process using data from both time steps to construct predictive models of the future spread of raccoons, increasing our utilization of available data. Data from both time steps were pooled to parameterize the dispersal kernel, which was then used to predict the probability of a district being dispersed to in 2006 and 2011. Districts that were already occupied were given a dispersal probability of one. These dispersal probabilities were used to weight two SDMs, one calibrated on 2006 distribution data and one calibrated on 2011 distribution data. The predictive performance of these SDMs was assessed by calculating the area under the receiver operating characteristic (ROC) curve, known as the AUC, a threshold independent measure of model skill (Swets 1988). AUC was calculated using the verification package (NCAR—Research Application Program 2007). AUC was calculated under cross-validation, where the data was repeatedly (1000 times) split into two parts, the training set (75 % of the data) used for fitting the SDM, and the testing set (remaining 25 % of the data) used to test the model performance. We note that this approach underestimates SDM skill when distributions are not at equilibrium, as models are penalized for predicting districts to be suitable when these districts are unoccupied due to dispersal limitation (Sullivan et al. 2012), so should be considered a minimum estimate of model performance. Predictions from the two SDMs contain some independent information (although some districts were occupied or unoccupied at both time points, others changed occupancy state, while the probability of a district being dispersed to also changed), and we lack strong a priori reasons for favoring one SDM over the other. We averaged the two predictions, as in such instances taking an average of predictions emphasizes signal where the model predictions are in agreement (Araújo and New 2007), to give a consensus prediction of habitat suitability.

Modelling the future distribution of the raccoon

We used a cellular automata simulation, implemented in R, to model the future spread of raccoons. This model assumes that the probability of a district becoming occupied is a function of the probability that it is suitable (given by the SDM) and the probability that it is dispersed to, which is assumed to be a function of distance from the nearest occupied district (given by the dispersal kernel). If these events are independent, than the probability of a district being occupied is the product of the probability of it being suitable and the probability of it being dispersed to. However, as the species distribution and dispersal models were parameterized separately, the estimated prevalence in one model (e.g. the SDM) will implicitly account for the other process (e.g. dispersal). While this does not affect the relative probabilities of occupancy obtained by multiplying the dispersal and suitability probabilities together, it will affect the absolute probabilities. Because of this it was necessary to calibrate these colonization probabilities by finding the threshold that minimized the number of difference between omission (false absence) and commission (false positive) errors (Jimenez-Valverde and Lobo 2007), assessed by running the model starting at the 2006 distribution to predict the 2011 distribution. Districts with colonization probabilities greater or equal to this threshold were classed as occupied. The cellular automata were run for ten time-steps from the current distribution, i.e. modelling the spread of raccoons up to 2061. This cellular automata model is deterministic, and the predicted pattern of spread can be thought of as our best estimate of spread given our parameterized dispersal kernel and SDM.

We explored the consequences of occasional colonization of districts with low colonization probabilities (e.g. due to long-distance dispersal) by running a separate, stochastic version of the simulation. This model differed from the deterministic model in that districts were classed as occupied if the colonization probability was greater or equal to a value drawn randomly form a uniform distribution, rather than a fixed threshold. We used a uniform distribution ranging from zero to twice the threshold used in the deterministic model (this upper limit means that 50 % of values drawn are expected to be greater than the threshold). The stochastic simulation was run 1000 times. The proportion of simulation runs an administrative district is colonized at a given period in time gives a measure of the risk that it will have been colonized.

Results

Current status of the raccoon in Germany based on hunting bag data

Since hunting started in 1954 in Hesse (HE), raccoon records have increased, with an exponential trend in the last decade (Fig. 1). Our data on raccoon distribution cover this period of conspicuous increase and allow us to study changes in density and distribution from 2000/01 to 2011/12 (Fig. 2, Online Resource Fig. S1). The highest raccoon bags can still be found around the initial release sites at the Edersee in HE and Wolfshagen in Brandenburg (BB). In the 2001/02 hunting season the records exceeded a density of 1 individual per 100 ha in the core area of the distribution, while in 2010/11 the hunting bag in the district of Höxter (HX) reached a maximum value of 3.2 per 100 ha. Although densities increased, the rate was slower in core areas than in parts of the range margin, with the strongest increase in districts between the introduction sites (Fig. 2). Several isolated populations appeared in the range margins in 2000/01 and seemed to establish in the following years (for example the colonization of Rhineland-Palatinate (RP) near the Luxembourg border and Baden-Württemberg (BW)).

Habitat suitability analysis

Following model selection, SDMs calibrated on both 2006 and 2011 distributions included a positive relationship between raccoon occurrence and the percentage of landscape in each district covered by agriculture (PLAND_C2) and a positive relationship with both the percentage of landscape covered by forest in each district (PLAND_C4) and the forest clumpiness index (CLUMPY_C4), the latter indicating a negative effect of forest fragmentation on raccoon occurrence. The SDM calibrated on the 2006 distribution also contained a positive association with the percentage of landscape in each district that was pasture and open areas (PLAND_C3), while a positive relationship with the clumpiness index of pasture and open areas (CLUMPY_C3) was included in the SDM calibrated on the distribution at the 2011 time step (Table 1).

Although differences in selection of variables in SDMs calibrated on distribution data from different time steps resulted in differences in the assessment of the favorability of each district, both models show a tendency to favor habitats between both introduction sites in Germany and exclude areas in North Rhine-Westphalia (NRW) and Bavaria (BY) (see Online Resource Fig. S2b).

Prediction of range expansions

Our modelling approach showed good short-term predictive power, with a model parametrized on data from the first time step correctly classifying the occupancy status of 92 % of districts in 2011 (and also showing good threshold independent performance, AUC = 0.93). The cellular automata, averaging the predicted suitability from the 2006 and 2011 calibrated SDMs (for results using the single SDMs see Online Resource Fig. S2), predicted that raccoons will occupy 252,940 km^2 in 2061 (Fig. 3a), with the dispersal kernel ($P = e^{-bx}$, see methods for definition) parameterized as $b = 0.031 \pm 0.002$ SE. Many districts that are not predicted to be colonized in the deterministic model were colonized in many iterations of the stochastic model (Fig. 3b), indicating that occasional colonization of districts with low suitability/dispersal probabilities has the potential to increase the speed of range expansion.

Discussion

Indirect measures of population density and population dynamics, such as harvest data, are often used to make inference on long term population dynamics when direct data are either not available or are logistically difficult to obtain, particularly at larger scales (Cattadori et al. 2003; Kitson 2004; Kerlin et al. 2007; Bosch et al. 2012). We use hunting bag data to

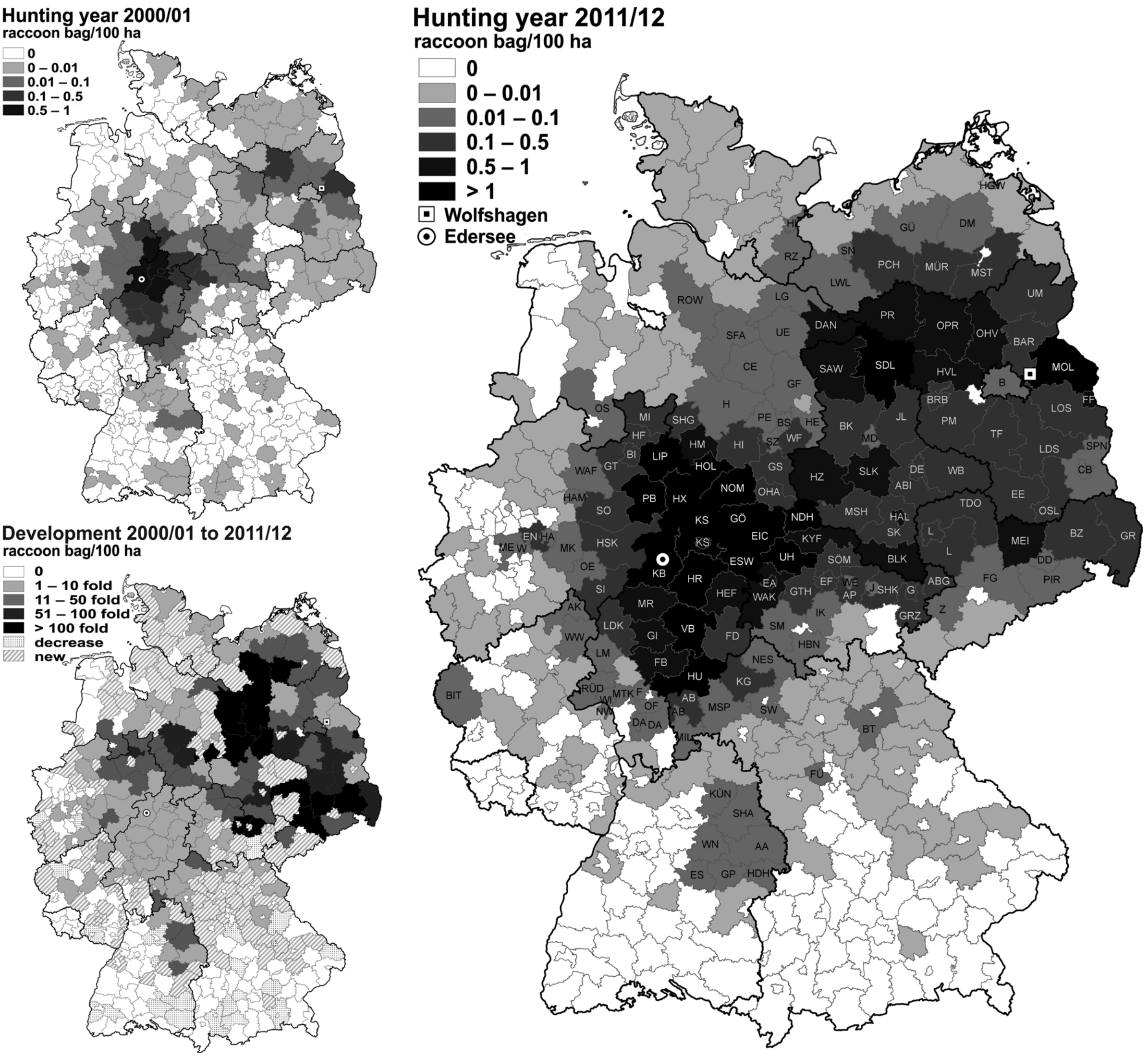

Fig. 2 Status and development of raccoon range expansion in Germany. Raccoon bag were calculated to 100 ha of the district areas for hunting years 2000/01 and 2011/12. The development map represents the change in the raccoon bag between both years

document the range expansion and increase in density of raccoons in Germany, illustrating its potential use for monitoring the status of alien species. Our analysis revealed that increases in density are not spatially uniform, with the strong increases in density in districts between release sites indicating that the merging of previously separate populations may play an important role in increasing the rate of expansion. We predict that raccoons will continue to expand, and will colonize most of Germany by the middle of the twenty-first century.

Using hunting bag data to monitor alien species

Although hunting records can provide a useful data, there are potential biases that should be considered. Hunting bags are dependent of hunting effort, which is dependent on the selection of harvesting locations, harvest strategy and hunting seasons, while both hunting effort and success can be affected by weather conditions (Engeman et al. 2013). These issues will be most severe if spatial variation in hunting effort changes as a species disperses. Additionally, data are

Table 1 Land-cover factors affecting the colonization process of raccoons in Germany

	2001–2006			2006–2011		
Explanatory variables	β	SE	Significance	β	SE	Significance
Intercept	−22.001	8.587	*	−29.050	8.223	***
PLAND_C2	0.074	0.030	*	0.048	0.019	*
PLAND_C3	0.125	0.062	*	–	–	–
PLAND_C4	0.053	0.034	n.s. (0.11)	0.051	0.023	*
C3_CLUMPY	–	–	–	7.672	5.743	n.s. (0.18)
C4_CLUMPY	19.322	9.158	*	24.013	7.840	**
	AIC = 35.38			AIC = 41.95 AUC = 0.804 ± 0.052 SD		
	AUC = 0.703 ± 0.08 SD					

The dispersal probability for each of the 412 administrative districts was used to weight the GLMs

Variables are abbreviated as follows: C2: agriculture, C3: pasture and open areas, C4: forests, PLAND: Percentage of landscape, CLUMPY: Clumpiness index; level of significance: *** $P < 0.001$; ** $P < 0.01$; * $P < 0.05$, *n.s.* not significant

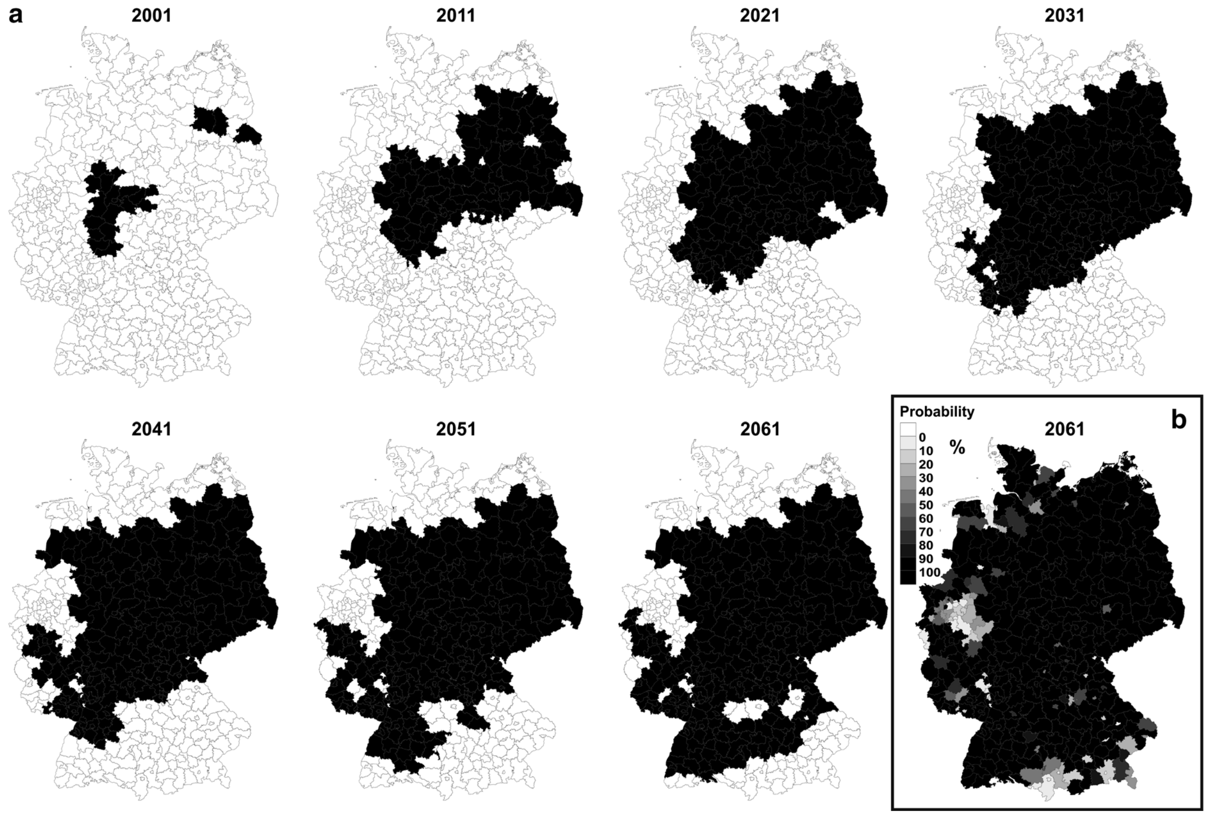

Fig. 3 Future raccoon range expansion in Germany. *a* Simulation of districts being dispersed to by different time points given by the deterministic model averaging suitability values. *b* Probability of districts being dispersed to in year 2061 given by the stochastic model

only available at district level resolution, and considerable heterogeneity raccoon abundance and environmental conditions within districts is highly likely. The ability to accurately assess the species environment relationship is likely to depend on the degree to which environmental variation between districts exceeds variation within districts. Variation in the size of districts means that the centroids of two neighboring large districts are further apart than those of two neighboring small districts, introducing uncertainty into measurements of distance used to parameterize the dispersal kernel that would be reduced if data were available in a uniform grid. Additionally, variation in district size may affect expansion dynamics; for example accelerating increases in the apparent area of occupancy could be driven by colonization of larger districts during range expansion. However, we found no relationship between district area and colonisation date, density or hunting bag development (Online Resource Fig. S3a–c), indicating that the larger mean district area in the northeastern part of Germany (Online Resource Fig. S3d) and other spatial variation in district size is unlikely to have introduced bias into our results. Despite the potential issues with district level hunting bag data, national-scale hunting data (available here across 357,557 km^2) provides an opportunity to examine population trends and study the patterns of range expansion that would not be possible with other datasets. Additionally, we show that such data can be used to construct SDMs with good predictive performance despite the coarse resolution of the input data.

Hunting bag data potentially has additional applications beyond assessing the spatial spread of non-native species. Hunting bag data are often available over long time-scales, providing a time-series of non-native species abundance rarely available from other monitoring methods. These time-series can be used to investigate interactions between invasive and native species (Brzeziński et al. 2010; Carlsson et al. 2010) and give key information for management implications (Koike 2006; Giovanelli et al. 2008; Saito et al. 2012).

Habitat associations of raccoons

We identified forests and agriculture as favored habitats for raccoons in models calibrated to both 2006 and 2011 distribution data, with the aggregation of woodland patches especially important for raccoon colonization (Table 1). This indicates that woodlands may act as corridors facilitating the spread of raccoons. Forests and agriculture have been identified as favored habitats in North America and Germany before, although agriculture seems to play a more important role in the native range, probably due to the greater extent of corn (an important food resource for raccoons) there (Pedlar et al. 1997; Winter 2004; Beasley et al. 2007).

Our results indicate that areas with a mixture of forest and agriculture are suitable for raccoons, with forest areas providing shelter and agricultural fields providing seasonal food resources. A study on songbird nest predation by raccoons (Chalfoun et al. 2002) indicates that raccoons were significantly more abundant in forest edges than in the forest interior, supporting the positive effect of landscape heterogeneity due to higher resource availability. On the other hand, the negative effect of forest fragmentation in our model was consistent with the finding for another invasive mammal that the potential for long-distance dispersal does not necessarily facilitate range expansion when availability of suitable habitat is fragmented (Fraser et al. 2015).

Deciduous forests are described as raccoons' original habitat in their native range (Kaufmann 1982), however, after splitting our forest class into the constituent CORINE broad-leaved, coniferous and mixed forests classes, we do not find a preference for deciduous forests. In addition wet habitats, also preferred in previous studies, had no significant effect in our models. These might be explained by the fact that both small waterside areas and different forest types are not fully reflected in the scale of the CORINE land-cover data, which only maps the most dominant habitat structure at a 100 meter resolution raster.

The differences between the SDMs at different time periods (see Table 1: PLAND_C3 and PLAND_C4) may reflect uncertainty about raccoon habitat associations, with the importance of different variables being sensitive to the additional data used in the 2011 model. Alternatively, there may have been a genuine shift in habitat preference, with less favorable habitats only becoming occupied as raccoons reach higher population densities. Such density-dependent shifts in habitat associations have been found in a wide range of species (Sullivan et al. 2015), indicating that habitat associations may not be constant throughout invasions. Rates of range expansion can increase as spatial sorting leads to expanding range margins being dominated by strong dispersers (Shine et al. 2011). Similarly, rates of spread can interact with habitat suitability, with landscape heterogeneity found to influence temporal and spatial variation in rates of range expansion in American Mink in Scotland (Fraser et al. 2015). This indicates that it is not always appropriate to assume constant parameters throughout the process of range expansion, highlighting the importance of future work investigating the interactions between dispersal and habitat suitability in order to refine future modelling efforts.

Patterns of dispersal

Our models predicted that many districts have suitable habitat, but currently have a low probability of being dispersed to. This suggests that the distribution of raccoons in Germany is strongly dispersal limited. The long lag phase and the slow expansion speed in the beginning of establishment may be explained by the philopatric behavior of the species (Gehrt and Fritzell 1998; Muschik et al. 2011). In the following expansion, the merging of different populations is likely to have combined genetic variation from multiple sources. This has been described as a key factor in previous successful invasions (Kolbe et al. 2008; Schulte et al. 2012), and may explain the accelerated invasion of the species, especially in the area between the introduction sites of Edersee in HE and Wolfshagen in BB (see Fig. 2). Beside the two commonly known introduction sites, it proved difficult to identify further introduction sites according to the hunting bag data. However, the registration of high harvest records in districts Harz (HZ) and Salzlandkreis (LK) in the Harz region as well as in Meißen (MEI), Bautzen (BZ) and Görlitz (GR) in the northeastern part of Saxony (SN) combined with the changes between 2000/01 and 2011/12 (Fig. 2) suggest that there indeed might be an additional influence of further introduced individuals, as has been recently discussed in genetic studies (Frantz et al. 2013; Fischer et al. 2015).

The stochastic simulation models consistently predicted a greater area to be dispersed to than the deterministic model. A key difference between both models is that in the stochastic version a district with low favorability or dispersal probability can be colonized by chance. This can enhance the spread of raccoons by enabling them to jump barriers posed by unfavorable districts. Additionally, occasional colonization of districts with low dispersal probabilities in the stochastic model mimics long distance dispersal events. Long-distance dispersal can explain accelerating range expansion (Shigesada et al. 1995), so the faster range expansion in the stochastic model may be due to greater emphasis on long-distance dispersal events than the deterministic model. Although not included in the model, a further aspect influencing the dispersal may be newly introduced individuals, especially in the range margin, as a study about the establishment of the raccoon in RP indicates (Fischer and Hohmann unpublished data).

In our model, districts within 22.6 km of the nearest occupied district had a probability of > 0.5 of being dispersed to over a 5 years time step, with this probability falling to 0.1 for districts 75 km from the nearest occupied district. This indicates considerably greater dispersal potential than found in a previous study comparing raccoon distribution at two time periods in Japan, where almost no colonization was observed at 10 km distance (Koike 2006). Population genetics studies investigating raccoon dispersal also suggest that most dispersal is short-range, with 85 % if raccoons moving <3 km (Cullingham et al. 2008). However, long-distance dispersal up to 42.4 km (Dharmarajan et al. 2009) and in a single case up to 285 km (Michler and Köhnemann, 2010) has been documented, and this combined with the cumulative movements of multiple generations of raccoons over a time step explains the dispersal potential predicted by our work.

A striking pattern from raccoon hunting bag data is that after over 60 years with a relatively stable population the density of raccoons increased dramatically in the 1990s, and is still increasing even around the original introduction sites (Fig. 1). This pattern of rapid increase in population/range-size with a long lag following introduction has been widely documented in invasive species (e.g. Shigesada et al. 1995), and has an important management implication as populations of invasive species may appear stable but can get quickly out of hand.

Management implications

Using a conservative estimate of 2–3 raccoons per 100 ha from a study in Müritz National Park (districts: MÜR, MST) in MV (Michler et al. 2008) and our documented annual hunting bags of 0.1–0.3 individuals per 100 ha in these districts in the same period, we estimate that hunting bag densities are about 10 % of the true population density. Applying this to the national hunting bag gives an estimate of about

700,000 raccoons in Germany. Annual raccoon bags are still increasing (see e.g. Bartel et al. 2012; DJV 2012; Arnold et al. 2013; this study), suggesting that even in the range core the carrying capacity may not yet have been reached. This highlights the potential for future population growth and an increasing impact of the species on native communities, ecosystems and economic life in Germany and Central Europe.

A number of negative impacts of raccoons on ecosystems in the non-native range have been suggested, but evidence from direct tests of these impacts is scarce (Lutz 1981; Gebhardt 1996; Kauhala 1996; Frantz et al. 2005). Suggested impacts include harm to native bird populations through nest predation (Günther and Hellmann 2002; Schrack 2010; García et al. 2012), negative impact on bats (Rasper 2000; Günther and Hellmann 2002), and predation of endangered reptiles such as hynobiid salamanders in Japan (Hayama et al. 2006), the European Pond Turtle (*Emys orbicularis)* in Germany (Schneeweiß and Wolf 2009) or the Spanish terrapin (*Mauremys leprosa)* (Álvarez 2008). We predicted continued range expansion into north-east Germany, where bogs and swamps hold relict populations of the critically endangered European pond turtle. Local management actions such as control programs may be necessary here to protect sensitive relict populations of native species from additional predation pressure. The growing population size, merging and the exchange of previously separated populations and geographic spread of raccoons in Europe, may increase the risk raccoons pose to human and animal health through the transmission of dangerous parasites or diseases, e.g. the canine distemper virus, the raccoon roundworm *Baylisascaris procyonis* or rabies (Sorvillo et al. 2002; Beltrán-Beck et al. 2012; Vos et al. 2012, 2013).

Our monitoring data of the dispersal history and status of the raccoon in Germany provide a framework to guide investigations of these potential negative impacts in the non-native range in Central Europe. The methods we have used (using hunting bag data to develop models of dispersal) could be applied to other systems to document and predict the spread of non-native species across large spatial scales. Such analyses will be needed to support decision making at national and European levels, for example allowing the risk of disease spread and biodiversity hazards as well as the feasibility of control measures to be assessed. The new Regulation (EU) No. 1143/2014 of the European Parliament and of the Council of 22 October 2014 on the prevention and management of the introduction and spread of invasive alien species places emphasis on understanding invasion pathways, so further studies documenting the dispersal of non-native species are urgently needed.

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Author contributions Marietta L. Fischer designed the study. Marietta L. Fischer, Martin J. P. Sullivan and José Guerrero-Casado analysed the data. Marietta L. Fischer, Grit Greiser, Mike Heddergott, Ulf Hohmann, Oliver Keuling, Johannes Lang, Ina Martin, Frank-Uwe Michler, Armin Winter and Roland Klein collected the data. Marietta L. Fischer and Martin J. P. Sullivan wrote the paper, with contributions from the other authors. Roland Klein supervised Marietta L. Fischer.

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