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

3 Keywords: Invasive species, Wildlife management, Species-environment relationship, Dispersal weighting,
4 Habitat favorability, Species distribution model

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33

34 **Abstract**

35 As the second largest cause of biodiversity loss worldwide, there is an urgent need to study the dynamics of
36 biological invasions and identify factors limiting the distribution of invasive alien species. In the present study
37 we analyze national-scale hunting bag data from Germany to predict the dispersal of raccoons in the largest non-
38 native population of the species. Our focus is (1) to document changes in the distribution and abundance of
39 raccoons, (2) to identify the species-environment relationship and predict which areas will be suitable for future
40 colonization and (3) to apply a dispersal model to predict how fast the raccoon will spread to these areas. The
41 increase from about 9,000 harvested raccoons in 2000/01 to about 71,000 in 2011/12 reflects the extensive
42 amount of suitable habitat for this omnivorous species in Central Europe. The best model for explaining range
43 expansion in Germany identified coverage of agriculture and fragmentation and coverage of forests as the most
44 important explanatory variables. The range of raccoons (area with harvest index > 0.1 per 100 ha) increased from
45 26,515 km² in 2001 to 111,630 km² in 2011, and is predicted to expand to 252,940 km² by 2061, 71 % of the
46 area of Germany. This vast area encompasses strategically important areas for conservation biology, such as
47 wetlands with endangered native terrapins. The combination of merging of separated introduced populations and
48 accelerating population growth highlights the potential for future impacts of raccoons on native communities,
49 ecosystems and economic life in Germany and Central Europe.

50 **Introduction**

51 Worldwide, Invasive Alien Species (IAS) are associated with significant damage to the economy and public
52 health, and are considered to be one of the major threats to native biodiversity (Mack et al. 2000; Pimentel et al.
53 2005; Hulme 2007; Pyšek and Richardson 2010; Keller et al. 2011). Hence a major challenge lies in determining
54 factors causing invasion success and predicting the potential distribution of non-native species. Wildlife
55 monitoring programs help to determine the distribution of non-native species, which is necessary in order to
56 assess the impact of non-native species in terms of disease risks, economic damage and negative effects on
57 native species and the environment, and plan management actions to reduce these impacts (Engeman et al. 2006;
58 Sterner and Smith 2006; Yokomizo et al. 2009). Monitoring programs for terrestrial mammals are usually based
59 on the collation of ad-hoc records (Roy et al. 2014a), systematic surveys of abundance (such as road-kill surveys,
60 tracking plots, spotlighting, pellet counts along fixed routes), or more cost intensive and logistically complicated
61 methods such as radio-tracking, mark-recapture, camera trapping, aerial surveys and DNA genotyping
62 (Woodroffe et al. 1990; Bartel et al. 2012; Engeman et al. 2013). Hunting bag data are routinely collected for

63 game species, and these offer an additional monitoring strategy as they can be used as a general index of long
64 term trends, population and distribution change and a proxy of abundance across time (Cattadori et al. 2003;
65 Kitson 2004; Carlsson et al. 2010).

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

80 Raccoons were introduced in different European countries by deliberate or accidental releases occurring
81 since the early twentieth century (Beltrán-Beck et al. 2012). They have become widely established, and are
82 considered a pest in several places due to the economic damage they cause, their threat to public health and
83 negative interactions (competition and predation) with native species (Ikeda et al. 2004; Beltrán-Beck et al.
84 2012; Vos et al. 2012, 2013). Additionally, they were identified as one of the top ten invasive alien species with
85 the greatest potential to threaten biodiversity in Great Britain (Roy et al. 2014b). In Europe the largest non-native
86 population is found in Germany, and is commonly assumed to stem from two separate founding events in
87 Central (1934, Edersee) and Northeast Germany (1945, Wolfshagen) (Stubbe 1975; Lutz 1984). Recent genetic
88 studies (Frantz et al. 2013; Fischer et al. 2015) propose an additional founder population in the federal state
89 Saxony near the Polish border and a further introduction event in the Harz region, which may influence the
90 distribution and abundance of raccoons in Central Europe (see Fig. 1).

91 Population densities in the native range are usually around 10 – 12 raccoons per 100 ha (Kaufmann 1982)
92 and can reach 333 individuals per 100 ha in urban sites (Riley 1998). Population densities in the non-native

93 range are lower than this, with the highest densities in swamp areas of Northeastern Germany (Müritz National
94 Park) with 6 – 8 individuals per 100 ha (Muschik et al. 2011) and in the urban areas of Bad Karlshafen and
95 Kassel in Central Germany where densities exceed 100 individuals per 100 ha (Hohmann and Bartussek 2011).
96 The forested Solling mountains probably provide the most comparable habitat to that typically occupied in the
97 native range, and population densities here are 1 – 4 individuals per 100 ha (Hohmann 1998). These lower
98 population densities to comparable habitat in the native range indicate the potential for future population growth
99 in Germany.

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

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

109 **Materials and Methods**

110 Hunting bag data as indicator for raccoon relative abundance

111 Although there are known problems related to the use of hunting statistics as population indexes (Hornell-
112 Willebrand et al. 2006; Ranta et al. 2008), several comparisons of census data and hunting bag statistics
113 suggested largely similar conclusions from both data sources (Baines and Hudson 1995; Cattadori et al. 2003;
114 Imperio et al. 2010 Knauer et al. 2010). Thus to analyze the population dynamics of raccoons in Germany,
115 annual hunting bag data at administrative district level (412 districts, status 2009), gathered up by the German
116 wildlife information system database (WILD), which is commissioned by the German Hunting Association
117 (Deutscher Jagdverband e.V.), were scanned for 12 hunting seasons from 2000/01 to 2011/12 (hunting seasons
118 cover the time from 1 April to 31 March). Hunting season for raccoons in Germany is open all year round except
119 for females nursing young and in the federal states Bremen and Saarland. Recordings include specimens found
120 dead and include both hunting in private and state owned land. The data were calculated relative to the total

121 district areas, which vary from 36 km² to 3,085 km², to give the density of records in each district. This allows
122 levels of invasion to be quantified consistently over the study area.

123 In 2007, 2008 and 2011 three district reforms have taken place in Germany, in the federal districts Saxony-
124 Anhalt, Saxony and Mecklenburg-Western Pomerania respectively. To assure comparable data we allocated the
125 records from the former Saxony-Anhalt and Saxony districts to the new districts, whereas we used the existing
126 borders of Mecklenburg-Western Pomerania from 2010. Where information was available, islands in the German
127 and the Baltic Sea were treated separately to the administrative districts they belonged to, as raccoons have so far
128 been unable to reach them. For hunting seasons from 2002/03 to 2007/08 as well as for the years 2010/11 and
129 2011/12 no information about the state hunting (1 – 5 % of the common raccoon bag) records was available for
130 the federal district Thuringia. Furthermore a lack of regional level harvest records existed for Saxony-Anhalt for
131 hunting years 2003/04 and 2004/05. Maps of district boundaries were created in the Geographical Information
132 Systems ArcGIS 10.1 (ESRI Inc, Redlands, CA, USA), using ESRI Data and Maps (2000, 2005) and infas
133 GEOdaten district borders (2009), projected to Transversal Mercator, Potsdam, Bessel.

134 In order to get a general idea about the raccoon range expansion, hunting bag data were arranged in the
135 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)
136 high, 0.5 – 1 and (6) very high, > 1 individuals per 100 ha. Sporadic records of single harvested raccoons are
137 likely to relate to transient individuals rather than established populations; we therefore converted all districts
138 with $x < 0.1$ raccoons per 100 ha to absent for the correlation and regression analysis. This approach focuses our
139 analysis onto highly suitable areas that we are confident hold established populations of raccoons, but by
140 potentially excluding some established populations with densities below this threshold our model predictions
141 will be more conservative than if we had classed all districts with raccoon records as occupied.

142

143 Explanatory variables of landscape structure

144 Macrohabitat characteristics of all 412 administrative districts were calculated on the basis of the CORINE
145 Land Cover (CLC2006 – 100m) using FRAGSTATS 4.1 (McGarigal et al. 2002). The original land cover
146 information containing 44 classes (37 classes for Germany) was reclassified into the following six habitat
147 classes, representing habitat classes considered potentially suitable for raccoons: artificial (C1), agriculture (C2),
148 pasture and open areas (C3), forests (C4), scrubland (C5) and wetlands and waterbodies (C6) (see Online
149 Resource Table S1). The effect of the environmental structure on the raccoon dispersal was analyzed at

150 vegetation-class level using the districts as sampling units. In order to characterize the habitat structure of the
151 districts, we used the following indices:

152 • Percentage of landscape (termed PLAND) quantified the proportional amount of each of the six
153 vegetation class types (C1 – C6) in the landscape on district level.

154 • Clumpiness index (termed CLUMPY) provides an effective index of fragmentation of patch types that
155 ranges from -1 when the patch type is maximally disaggregated to 1 when the patch type is maximally
156 clumped.

157

158 Calculating dispersal probabilities

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

$$168 \text{logit}(P) = \log(P/1-P) = \log(e^{-bx}/(1 - e^{-bx})).$$

169 This was then substituted into a binomial likelihood function,

$$170 \text{likelihood} = \sum -y \cdot \log(1 + e^P) - ((1 - y) \cdot (1 + e^P)),$$

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

176

177 Habitat suitability analysis

178 All land-cover variables for the model were checked for their independence by running a collinearity
179 procedure in IBM SPSS Statistics Version 21 (Pearson correlation $r < 0.7$; variance inflation factor < 3) and as a
180 result, the variable PLAND_1 was excluded from the analysis. We applied a logistic binominal generalized
181 linear model (GLM) in R, including the vector of dispersal probabilities as prior weights. This weighting reduces
182 the influence of areas that are unlikely to have been dispersed to, and has been shown to improve the ability of
183 species distribution models to characterize the species environment relationship of species that are not at
184 equilibrium with their environment (Sullivan et al. 2012). For the selection of the most parsimonious model we
185 used the stepAIC function from the MASS package (Venables and Ripley 2002) to remove covariates from
186 SDMs in a stepwise fashion based on the Akaike information criterion. Absolute predicted probabilities of
187 occurrence are sensitive to a species' prevalence, so we used the inverse of logit transformation (Real et al.
188 2006) to calculate the environmental favorability function for or against the species presence.

$$189 F = e^y / (n_1/n_0 + e^y)$$

$$190 \text{ with } y = \ln(n_1/n_0) + \alpha + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n$$

191 where α is a constant, n_1/n_0 = presence/absence ratio and $\beta_1, \beta_2, \dots, \beta_n$ are the coefficients of the n predictor
192 variables x_1, x_2, \dots, x_n . We modified the function to account for dispersal weighting by replacing n_1/n_0 by
193 $n_1/(n_0 \cdot \Sigma P)$.

194

195 Calibration and validation of models

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

208 hunting effort, while differences in distribution between time steps primarily reflects genuine changes in
209 distribution.

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

232

233 Modelling the future distribution of the raccoon

234 We used a cellular automata simulation, implemented in R, to model the future spread of raccoons. This
235 model assumes that the probability of a district becoming occupied is a function of the probability that it is
236 suitable (given by the SDM) and the probability that it is dispersed to, which is assumed to be a function of
237 distance from the nearest occupied district (given by the dispersal kernel). If these events are independent, than

238 the probability of a district being occupied is the product of the probability of it being suitable and the
239 probability of it being dispersed to. However, as the species distribution and dispersal models were
240 parameterized separately, the estimated prevalence in one model (e.g. the SDM) will implicitly account for the
241 other process (e.g. dispersal). While this does not affect the relative probabilities of occupancy obtained by
242 multiplying the dispersal and suitability probabilities together, it will affect the absolute probabilities. Because of
243 this it was necessary to calibrate these colonization probabilities by finding the threshold that minimized the
244 number of difference between omission (false absence) and commission (false positive) errors (Jimenez-
245 Valverde and Lobo 2007), assessed by running the model starting at the 2006 distribution to predict the 2011
246 distribution. Districts with colonization probabilities greater or equal to this threshold were classed as occupied.
247 The cellular automata were run for ten time-steps from the current distribution, i.e. modelling the spread of
248 raccoons up to 2061. This cellular automata model is deterministic, and the predicted pattern of spread can be
249 thought of as our best estimate of spread given our parameterized dispersal kernel and SDM.

250 We explored the consequences of occasional colonization of districts with low colonization probabilities (e.g.
251 due to long-distance dispersal) by running a separate, stochastic version of the simulation. This model differed
252 from the deterministic model in that districts were classed as occupied if the colonization probability was greater
253 or equal to a value drawn randomly from a uniform distribution, rather than a fixed threshold. We used a uniform
254 distribution ranging from zero to twice the threshold used in the deterministic model (this upper limit means that
255 50 % of values drawn are expected to be greater than the threshold). The stochastic simulation was run 1000
256 times. The proportion of simulation runs an administrative district is colonized at a given period in time gives a
257 measure of the risk that it will have been colonized.

258 **Results**

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

260 Since hunting started in 1954 in Hesse (HE), raccoon records have increased, with an exponential trend in the
261 last decade (Fig. 1). Our data on raccoon distribution cover this period of conspicuous increase and allow us to
262 study changes in density and distribution from 2000/01 to 2011/12 (Fig. 2, Online Resource Fig. S1). The
263 highest raccoon bags can still be found around the initial release sites at the Edersee in HE and Wolfshagen in
264 Brandenburg (BB). In the 2001/02 hunting season the records exceeded a density of 1 individual per 100 ha in
265 the core area of the distribution, while in 2010/11 the hunting bag in the district of Höxter (HX) reached a
266 maximum value of 3.2 per 100 ha. Although densities increased, the rate was slower in core areas than in parts of

267 the range margin, with the strongest increase in districts between the introduction sites (Fig. 2). Several isolated
268 populations appeared in the range margins in 2000/01 and seemed to establish in the following years (for
269 example the colonization of Rhineland-Palatinate (RP) near the Luxembourg border and Baden-Württemberg
270 (BW)).

271

272 Habitat suitability analysis

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

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

285

286 Prediction of range expansions

287 Our modelling approach showed good short-term predictive power, with a model parametrized on data from
288 the first time step correctly classifying the occupancy status of 92 % of districts in 2011 (and also showing good
289 threshold independent performance, AUC = 0.93). The cellular automata, averaging the predicted suitability
290 from the 2006 and 2011 calibrated SDMs (for results using the single SDMs see Online Resource Fig. S2),
291 predicted that raccoons will occupy 252,940 km² in 2061 (Fig. 3a), with the dispersal kernel ($P = e^{-bx}$, see
292 methods for definition) parameterized as $b = 0.031 \pm 0.002$ SE. Many districts that are not predicted to be
293 colonized in the deterministic model were colonized in many iterations of the stochastic model (Fig. 3b),
294 indicating that occasional colonization of districts with low suitability/dispersal probabilities has the potential to
295 increase the speed of range expansion.

296 **Discussion**

297 Indirect measures of population density and population dynamics, such as harvest data, are often used to
298 make inference on long term population dynamics when direct data are either not available or are logistically
299 difficult to obtain, particularly at larger scales (Cattadori et al. 2003; Kitson 2004; Kerlin et al. 2007; Bosch et al.
300 2012). We use hunting bag data to document the range expansion and increase in density of raccoons in
301 Germany, illustrating its potential use for monitoring the status of alien species. Our analysis revealed that
302 increases in density are not spatially uniform, with the strong increases in density in districts between release
303 sites indicating that the merging of previously separate populations may play an important role in increasing the
304 rate of expansion. We predict that raccoons will continue to expand, and will colonize most of Germany by the
305 middle of the 21st century.

306

307 Using hunting bag data to monitor alien species

308 Although hunting records can provide a useful data, there are potential biases that should be considered.
309 Hunting bags are dependent of hunting effort, which is dependent on the selection of harvesting locations,
310 harvest strategy and hunting seasons, while both hunting effort and success can be affected by weather
311 conditions (Engeman et al. 2013). These issues will be most severe if spatial variation in hunting effort changes
312 as a species disperses. Additionally, data are only available at district level resolution, and considerable
313 heterogeneity raccoon abundance and environmental conditions within districts is highly likely. The ability to
314 accurately assess the species environment relationship is likely to depend on the degree to which environmental
315 variation between districts exceeds variation within districts. Variation in the size of districts means that the
316 centroids of two neighboring large districts are further apart than those of two neighboring small districts,
317 introducing uncertainty into measurements of distance used to parameterize the dispersal kernel that would be
318 reduced if data were available in a uniform grid. Additionally, variation in district size may affect expansion
319 dynamics; for example accelerating increases in the apparent area of occupancy could be driven by colonization
320 of larger districts during range expansion. However, we found no relationship between district area and
321 colonisation date, density or hunting bag development (Online Resource Fig. S3a-c), indicating that the larger
322 mean district area in the northeastern part of Germany (Online Resource Fig. S3d) and other spatial variation in
323 district size is unlikely to have introduced bias into our results. Despite the potential issues with district level
324 hunting bag data, national-scale hunting data (available here across 357,557 km²) provides an opportunity to
325 examine population trends and study the patterns of range expansion that would not be possible with other

326 datasets. Additionally, we show that such data can be used to construct SDMs with good predictive performance
327 despite the coarse resolution of the input data.

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

333

334 Habitat associations of raccoons

335 We identified forests and agriculture as favored habitats for raccoons in models calibrated to both 2006 and
336 2011 distribution data, with the aggregation of woodland patches especially important for raccoon colonization
337 (Table 1). This indicates that woodlands may act as corridors facilitating the spread of raccoons. Forests and
338 agriculture have been identified as favored habitats in North America and Germany before, although agriculture
339 seems to play a more important role in the native range, probably due to the greater extent of corn (an important
340 food resource for raccoons) there (Pedlar et al. 1997; Winter 2004; Beasley 2007).

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

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

354 The differences between the SDMs at different time periods (see Table1: PLAND_C3 and PLAND_C4) may
355 reflect uncertainty about raccoon habitat associations, with the importance of different variables being sensitive

356 to the additional data used in the 2011 model. Alternatively, there may have been a genuine shift in habitat
357 preference, with less favorable habitats only becoming occupied as raccoons reach higher population densities.
358 Such density-dependent shifts in habitat associations have been found in a wide range of species (Sullivan et al.
359 2015), indicating that habitat associations may not be constant throughout invasions. Rates of range expansion
360 can increase as spatial sorting leads to expanding range margins being dominated by strong dispersers (Shine et
361 al. 2011). Similarly, rates of spread can interact with habitat suitability, with landscape heterogeneity found to
362 influence temporal and spatial variation in rates of range expansion in American Mink in Scotland (Fraser et al.
363 2015). This indicates that it is not always appropriate to assume constant parameters throughout the process of
364 range expansion, highlighting the importance of future work investigating the interactions between dispersal and
365 habitat suitability in order to refine future modelling efforts.

366

367 Patterns of dispersal

368 Our models predicted that many districts have suitable habitat, but currently have a low probability of being
369 dispersed to. This suggests that the distribution of raccoons in Germany is strongly dispersal limited. The long
370 lag phase and the slow expansion speed in the beginning of establishment may be explained by the philopatric
371 behavior of the species (Gehrt and Fritzell 1998; Muschik et al. 2011). In the following expansion, the merging
372 of different populations is likely to have combined genetic variation from multiple sources. This has been
373 described as a key factor in previous successful invasions (Kolbe et al. 2004; Schulte et al. 2012), and may
374 explain the accelerated invasion of the species, especially in the area between the introduction sites of Edersee in
375 HE and Wolfshagen in BB (see Fig. 2). Beside the two commonly known introduction sites, it proved difficult to
376 identify further introduction sites according to the hunting bag data. However, the registration of high harvest
377 records in districts Harz (HZ) and Salzlandkreis (LK) in the Harz region as well as in Meißen (MEI), Bautzen
378 (BZ) and Görlitz (GR) in the northeastern part of Saxony (SN) combined with the changes between 2000/01 and
379 2011/12 (Fig. 2) suggest that there indeed might be an additional influence of further introduced individuals, as
380 has been recently discussed in genetic studies (Frantz et al. 2013; Fischer et al. 2015).

381 The stochastic simulation models consistently predicted a greater area to be dispersed to than the
382 deterministic model. A key difference between both models is that in the stochastic version a district with low
383 favorability or dispersal probability can be colonized by chance. This can enhance the spread of raccoons by
384 enabling them to jump barriers posed by unfavorable districts. Additionally, occasional colonization of districts
385 with low dispersal probabilities in the stochastic model mimics long distance dispersal events. Long-distance

386 dispersal can explain accelerating range expansion (Shigesada et al. 1995), so the faster range expansion in the
387 stochastic model may be due to greater emphasis on long-distance dispersal events than the deterministic model.
388 Although not included in the model, a further aspect influencing the dispersal may be newly introduced
389 individuals, especially in the range margin, as a study about the establishment of the raccoon in RP indicates
390 (Fischer and Hohmann unpublished data).

391 In our model, districts within 22.6 km of the nearest occupied district had a probability of > 0.5 of being
392 dispersed to over a five year time step, with this probability falling to 0.1 for districts 75 km from the nearest
393 occupied district. This indicates considerably greater dispersal potential than found in a previous study
394 comparing raccoon distribution at two time periods in Japan, where almost no colonization was observed at
395 10 km distance (Koike 2006). Population genetics studies investigating raccoon dispersal also suggest that most
396 dispersal is short-range, with 85 % of raccoons moving < 3 km (Cullingham et al. 2008). However, long-distance
397 dispersal up to 42.4 km (Dharmarajan et al. 2009) and in a single case up to 285 km (Michler and Köhnemann,
398 2010) has been documented, and this combined with the cumulative movements of multiple generations of
399 raccoons over a time step explains the dispersal potential predicted by our work.

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

405

406 Management implications

407 Using a conservative estimate of 2 – 3 raccoons per 100 ha from a study in Müritzer National Park (districts:
408 MÜR, MST) in MV (Michler et al. 2008) and our documented annual hunting bags of 0.1 – 0.3 individuals per
409 100 ha in these districts in the same period, we estimate that hunting bag densities are about 10 % of the true
410 population density. Applying this to the national hunting bag gives an estimate of about 700,000 raccoons in
411 Germany. Annual raccoon bags are still increasing (see e.g. Bartel et al. 2012; DJV 2012; Arnold et al. 2013; this
412 study), suggesting that even in the range core the carrying capacity may not yet have been reached. This
413 highlights the potential for future population growth and an increasing impact of the species on native
414 communities, ecosystems and economic life in Germany and Central Europe.

415 A number of negative impacts of raccoons on ecosystems in the non-native range have been suggested, but
416 evidence from direct tests of these impacts is scarce (Lutz 1981; Gebhardt 1996; Kauhala 1996; Frantz et al.
417 2005). Suggested impacts include harm to native bird populations through nest predation (Günter and Hellmann
418 2002; Schrack 2010; García et al. 2012), negative impact on bats (Rasper 2000; Günter and Hellmann 2002), and
419 predation of endangered reptiles such as hynobiid salamanders in Japan (Hayama et al. 2006), the European
420 Pond Turtle (*Emys orbicularis*) in Germany (Schneeweiß and Wolf 2009) or the Spanish terrapin (*Mauremys*
421 *leprosa*) (Álvarez 2008). We predicted continued range expansion into north-east Germany, where bogs and
422 swamps hold relict populations of the critically endangered European pond turtle. Local management actions
423 such as control programs may be necessary here to protect sensitive relict populations of native species from
424 additional predation pressure. The growing population size, merging and the exchange of previously separated
425 populations and geographic spread of raccoons in Europe, may increase the risk raccoons pose to human and
426 animal health through the transmission of dangerous parasites or diseases, e.g. the canine distemper virus, the
427 raccoon roundworm *Baylisascaris procyonis* or rabies (Sorvillo et al. 2002; Beltrán-Beck et al. 2012; Vos et al.
428 2012, 2013).

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

438

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629 **Data Accessibility**

630 Database (hunting bag data, land-cover factors, SDMs) “database.xlsx”
631 Hunting bag data of Fig. 1 “hunting bag_Germany.xlsx”

632 **Author Contributions**

633 MLF designed the study. MLF, MJPS and JGC analysed the data. MLF, GG, MH, UH, OK, JL, IM, FUM, AW
634 and RK collected the data. MLF and MJPS wrote the paper, with contributions from the other authors. RK
635 supervised MLF.

636 **Figure Legends**

637 Fig. 1: Starting points, hunting start dates and change in raccoon populations in Germany. a) Grey lines and bold
638 letters represent the boundaries and abbreviation of the German federal states respectively: BB Brandenburg, BL
639 Berlin, BW Baden-Württemberg, BY Bavaria, HB Bremen, HE Hesse, HH Hamburg, MV Mecklenburg-
640 Western Pomerania, NI Lower Saxony, NRW North Rhine-Westphalia, RP Rhineland-Palatinate, SH Schleswig-
641 Holstein, SL Saarland, SN Saxony, ST Saxony-Anhalt, TH Thuringia. The years give information when the

642 raccoon was declared a game species in each federal state (Hohmann and Bartussek 2011). Edersee and
643 Wolfshagen indicate the geographic locations of the two introduced populations in 1934 and 1945. In the Harz
644 region and SN additional founder population were proposed (Frantz et al. 2013; Fischer et al. 2015). Black
645 points represent the location studies revealing raccoon densities, in the urban habitats of Kassel and Bad
646 Karlshafen in HE, in the low mountain forests in Solling in NI and in the swamp areas in Müritz in MV. (b) The
647 collected harvest records suggest an exponential trend in the last decade. Our study covers the strong increase
648 beginning in 2000.

649

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

653

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

657

658 Online Resource Fig. S1

659 Status and development of raccoon range expansion in Germany for hunting seasons 2001/02 to 2010/11.

660

661 Online Resource Fig. S2

662 Dispersal kernel, SDMs and simulation of raccoon range expansion in Germany for the individual models of
663 2006 and 2011. a) Dispersal kernel: circles: dispersal model predictions (larger circles denote higher dispersal
664 probabilities); black circles: occupied in the previous five-year time step; shading in dispersal maps represent the
665 hunting bag with white, 0; light grey, 0 – 0.01; grey, 0.01 – 0.1; and dark grey, $x > 0.1$; b) SDMs: habitat
666 favorability with white, 0 – 0.25; light grey, 0.25 – 0.5; grey, 0.5 – 0.75 and dark grey 0.75 – 1. c) Predictions of
667 raccoon range expansion for the years 2021, 2031, 2041, 2051 and 2061.

668

669 Online Resource Fig. S3

670 Spatial variation in district size and model parameters of spread. 3a) colonization date relative to district area 3b)
671 density relative to district area 3c) development relative to district area 3d) range of district sizes in the 16

672 federal states in Germany, sorted from West to East. Vertical lines represent the range from minimum district
673 area to maximum district area, horizon lines indicate the district's mean value included the standard deviation.

674

675

676 **Table and Figures**

677 Table 1: Land-cover factors affecting the colonization process of raccoons in Germany. The dispersal probability
 678 for each of the 412 administrative districts was used to weight the GLMs.

Explanatory variables	2001-2006			2006-2011		
	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 AUC = 0.703 ± 0.08 SD			AIC = 41.95 AUC = 0.804 ± 0.052 SD		

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

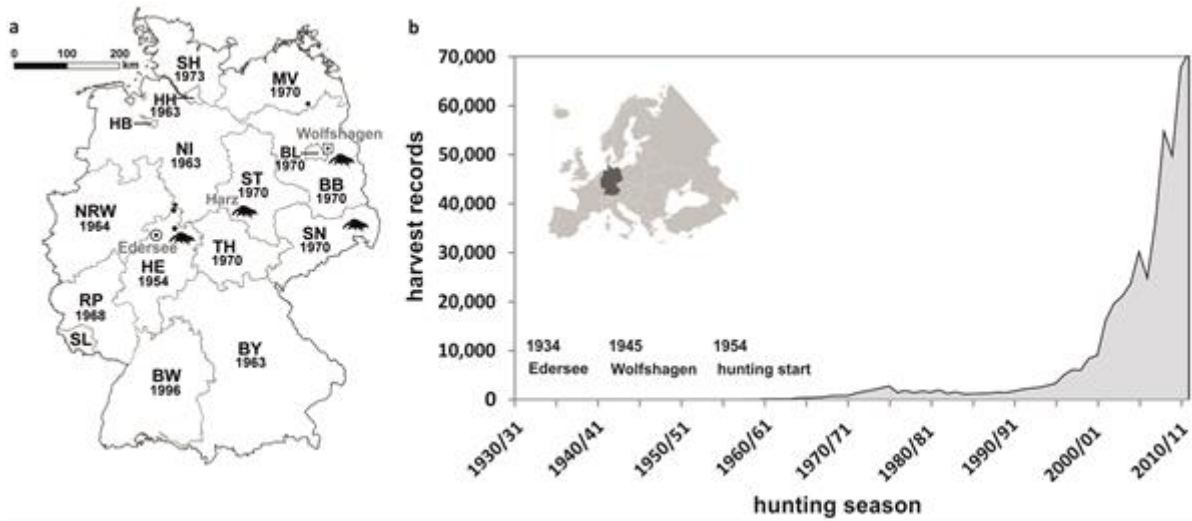
681 Table S1: Reclassification of Corine land-cover classes (CLC2006) into groups used in this analysis.

vegetation class	habitat category	CLC_Code
C1	artificial	111, 112, 121, 122, 123, 124, 131, 132, 133, 141, 142
C2	agriculture	211, 221, 222, 242, 243
C3	pasture and open areas	231, 331, 332, 333, 335
C4	forests	311, 312, 313
C5	scrubland	321, 322, 324
C6	wetlands and waterbodies	411, 412, 421, 423, 511, 512, 521, 522, 523

682

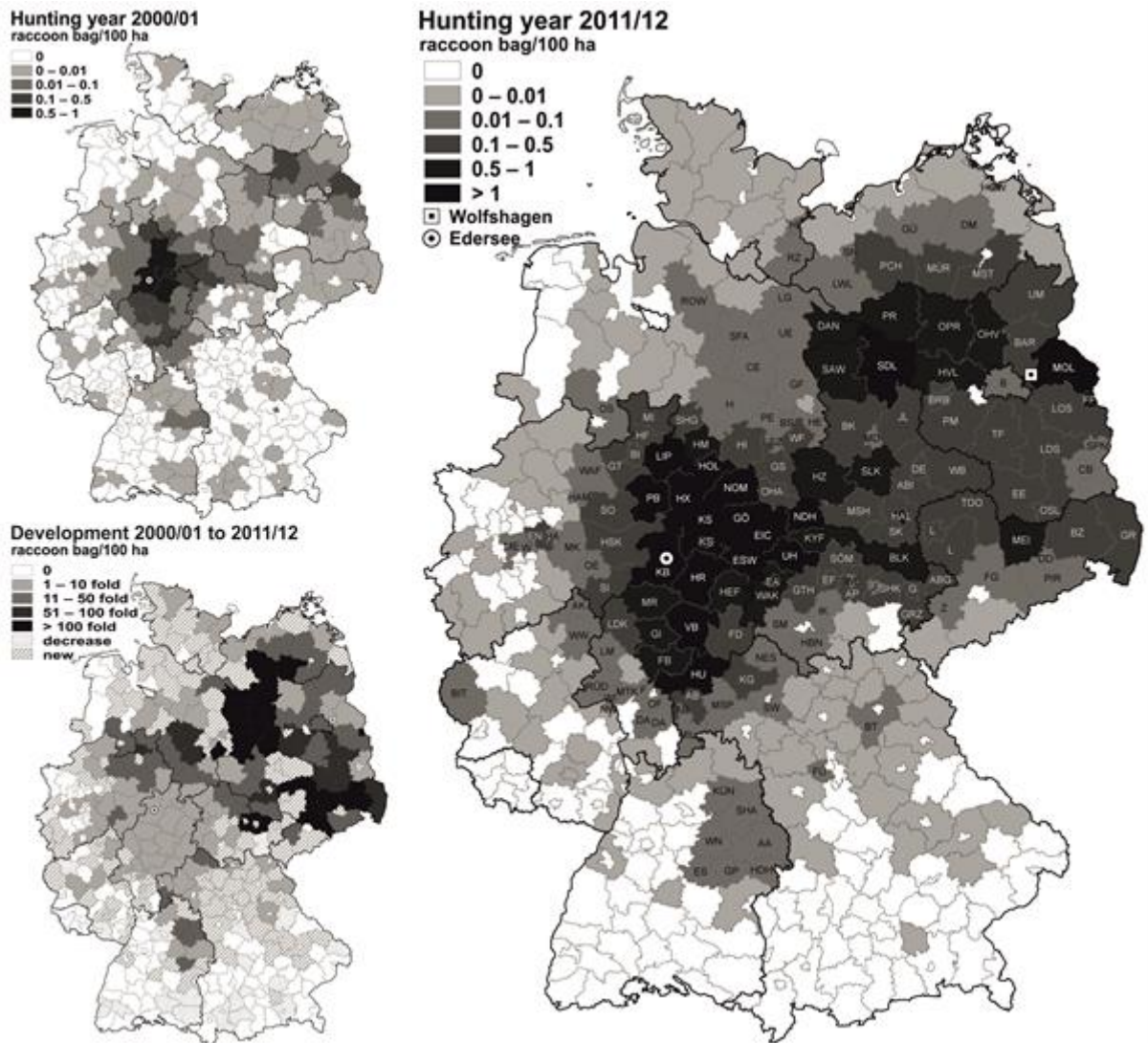
683 **Figures**

684 **Fig. 1**



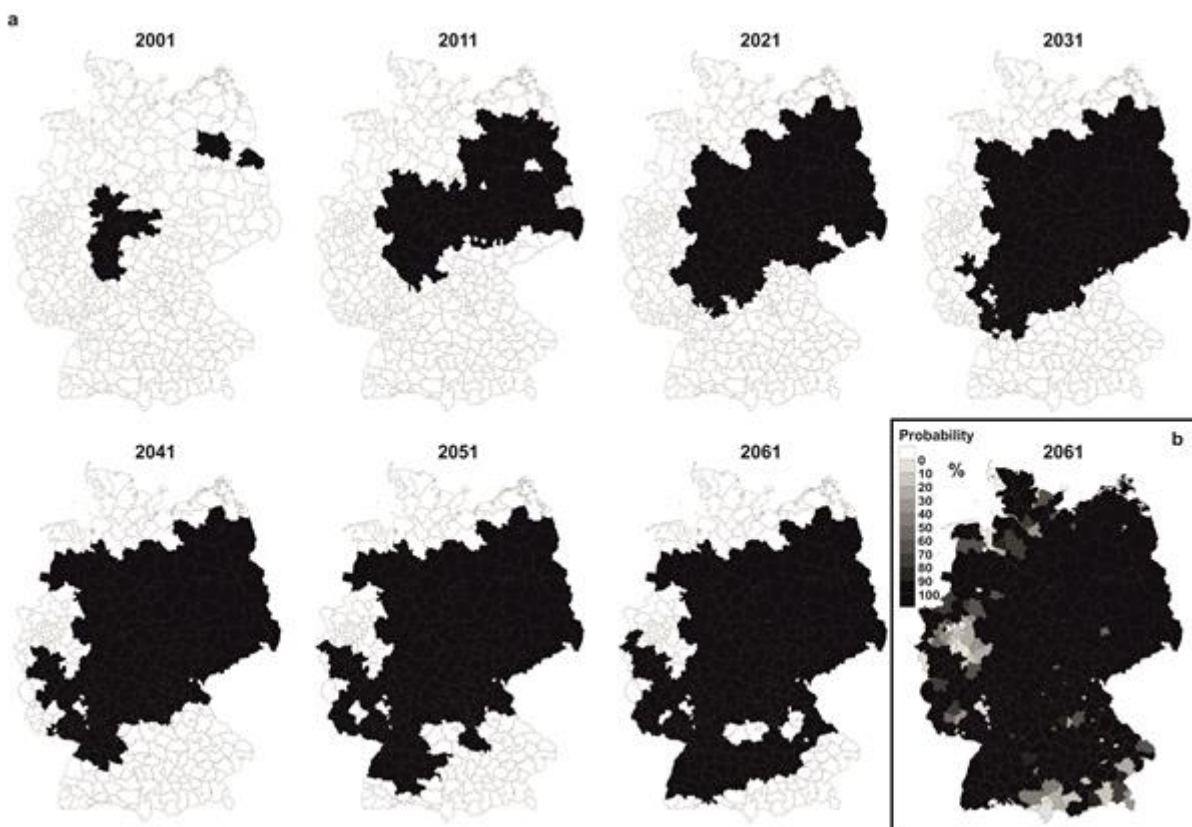
685

686 Fig. 2

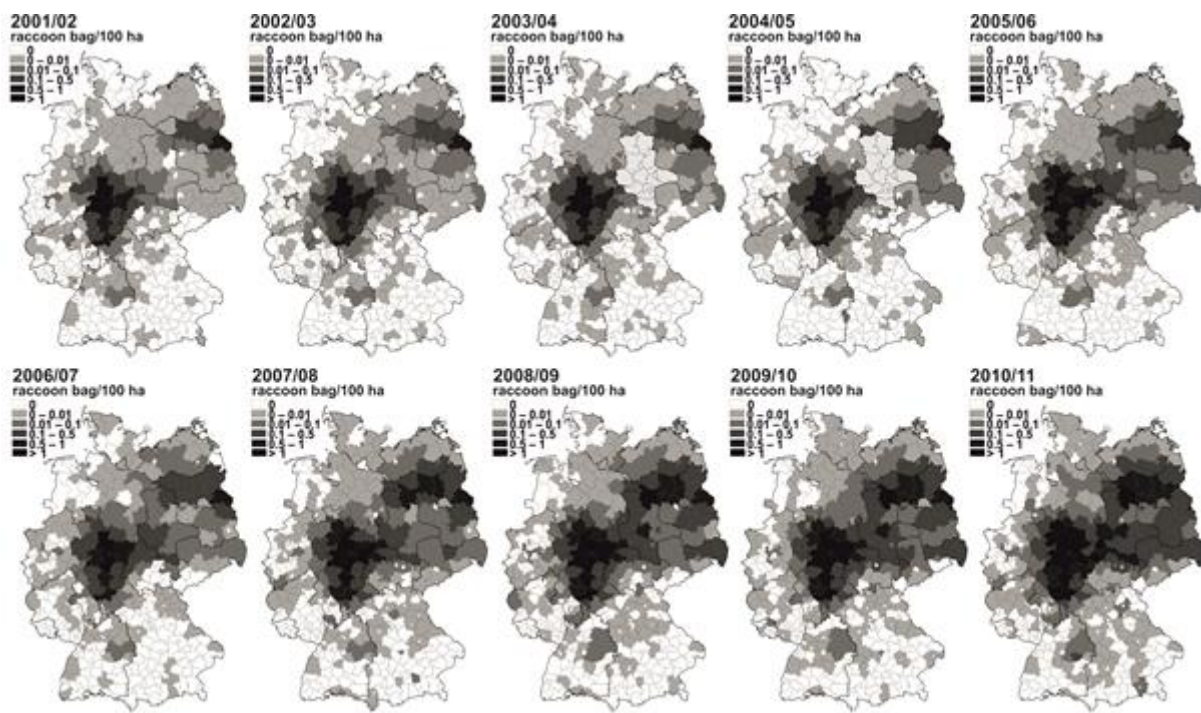


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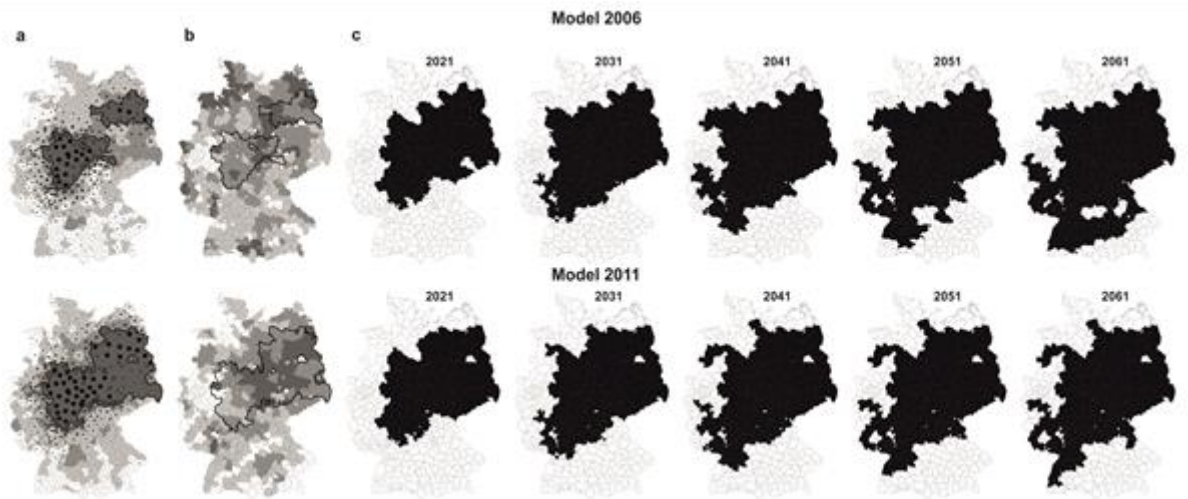
688 Fig. 3



690 Fig. S1

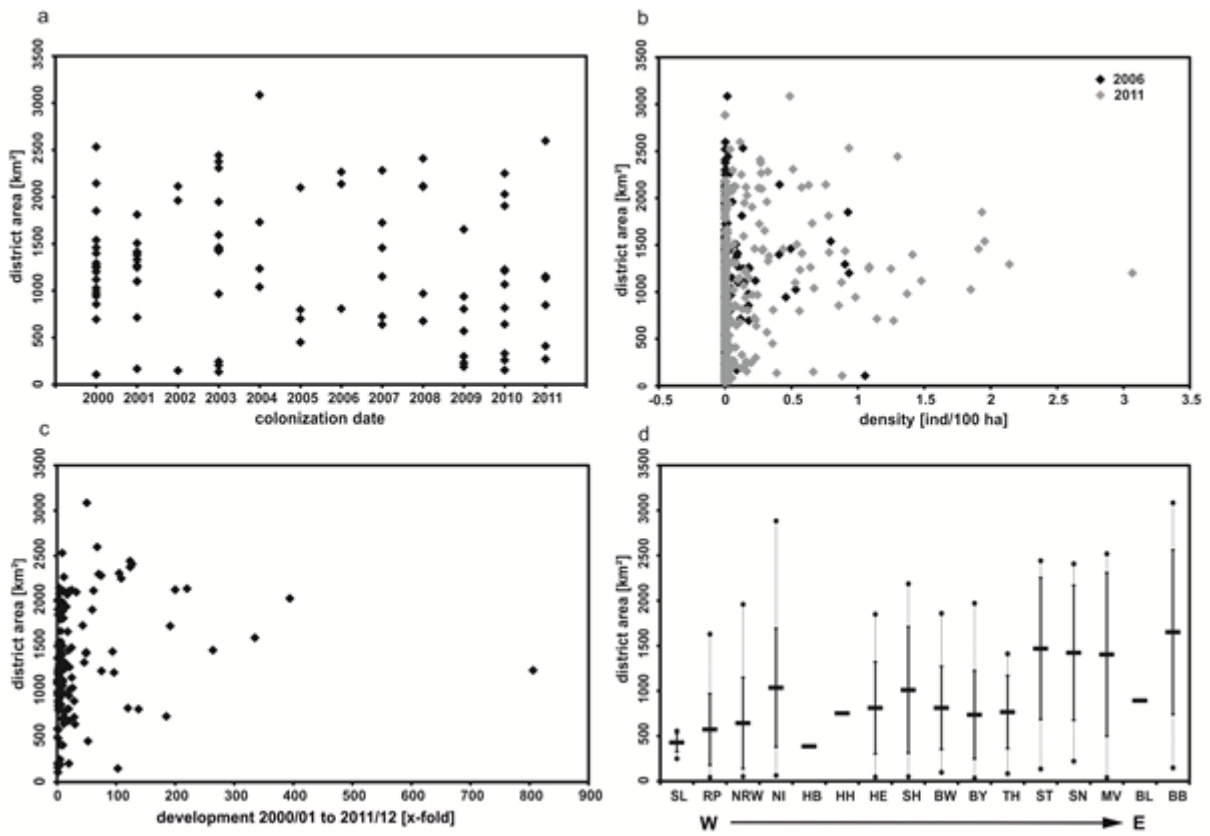


692 Fig. S2



693

694 Fig. S3



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