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European badger habitat requirements in the Netherlands – combining ecological niche models with neighbourhood analysis

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European badger populations in the Netherlands suffered strong declines in the 1900s, becoming endangered in the 1980s. Despite mitigation actions, recovery of the population has been slow. Here, we use ecological niche modelling, relating 1515 badger sett (burrow) localities to data on topographic, groundwater table, soil type and land-cover variables, to investigate the factors defining badger habitat suitability. Niche modelling of mobile animals such as badgers is challenging, as relevant features that determine habitat suitability surrounding animal sightings or burrow locations are often unaccounted for. In this study, habitat properties of the entire home range of individuals were incorporated via neighbourhood analysis on land-cover variables. The neighbourhood analysis was applied at different spatial scales, to assess maximum model fit at the scale most representative of badger home-range area in the Netherlands, which was approximately 3.6 km^2. Our results showed that marine and river clay render highly unsuitable habitat for badgers. Grassland and maize crops presence, typically reported as driving factors, had little effect on badger distribution in the Netherlands. Instead, moderate vegetation cover, remoteness from urban infrastructures and low groundwater tables resulted in optimal conditions. We conclude that food availability is not a limiting factor for badgers in the Netherlands, but rather appropriate soil conditions for sett digging and non-urban landscapes with sufficient cover for hideout determine their distribution. Our predictions indicate suitable areas that are not currently colonized. The results presented have important implications for management and conservation strategies in the Netherlands. Furthermore, we provide a useful general approach for niche modelling of mobile animals.

European badger *Meles meles* populations in the Netherlands have suffered strong declines over the past century. In the early 1900s, there were an estimated 2500–3000 badger setts (i.e. badger burrows or dens) and around 4000 individuals, which, by the 1960s, had declined to 900 occupied setts and 2200 badgers (Wiertz and Vink 1986). The population size reached its lowest point in the 1980s with only 560 occupied setts and an estimated 1400 individuals remaining, when the species became highly threatened in the Netherlands (van Wijngaarden et al. 1971, Wiertz and Vink 1986, van der Zee et al. 1992). During this period, the distribution of badgers was reduced to only a few disconnected populations (van Moll 2005). The factors underpinning this strong decline were both direct and indirect, including hunting, poaching, vehicle strikes, habitat loss and fragmentation, disturbance of existing setts and pollution (van Wijngaarden and van de Peppel 1964, Wiertz and Vink 1986, van der Zee et al. 1992, Dekker and Bekker 2010).

The threatened status of the badger in the Netherlands led to the implementation of a series of management strategies aiming to restore populations (Beheersoverleg Dassen 1983, Sneep 1986). These included habitat protection and rehabilitation, reintroductions, farmer indemnification, education programs and construction of ecoducts, fauna-tunnels and fences along roads to address fragmentation and reduce vehicle strikes (Sneep 1986, Dekker and Bekker 2010). Following implementation of these measures, badger populations increased significantly, with populations recovering to 2570 occupied setts in 2001, and resulting in removal of the species' threatened status (Wiertz 1993, van Moll 1999, 2002, 2005, van Apeldoorn et al. 2006, Witte et al. 2008). Despite this, badger re-occupation rates have been slow, with large areas of what is typically considered suitable habitat remaining unoccupied to date (Hollander and

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La Haye 2014). This raises the question of what the habitat requirements of badgers nowadays are in the Netherlands, a highly man-engineered country with dense human populations.

The European badger is a highly adaptive, generalist species with varying habitat requirements with respect to the landscape features it inhabits (Piza-Roca et al. 2014). Along its distribution through central, northern and western Europe, badger habitat requirements generally consist of a combination of earthworm-rich grassland, maize crops and woodland (Skinner et al. 1991, da Silva et al. 1993, Brøseth et al. 1997, Jepsen et al. 2005, Etherington et al. 2009). In eastern Europe, woodland is regarded as the most important factor influencing badger distribution (Matyáštík and Bičík 1999, Kowalczyk et al. 2000, 2003). In southern Europe, in arid, shrub-dominated Mediterranean landscapes, badger distribution is driven by different factors again, which include terrain suitability for sett digging, primary productivity and abundance of fruit and diverse prey items (Martín et al. 1995, Rosalino et al. 2005, Lara-Romero et al. 2012, Requena-Mullor et al. 2014). In the Netherlands, it has been assumed that, similar to other western and central European countries, grassland, maize crops and woodland are crucial elements for badgers. This assumption has received some support from a local study, which found that grassland, followed by woodland and maize crops were preferred landscape elements of badger populations in that area (van Apeldoorn et al. 2006). However, given the local scale of the study, these findings may not be representative of badger requirements for the entire country, especially given the high adaptability of this species. To date, a national evaluation of badger habitat requirements in the Netherlands is lacking, and is urgent for appropriate management of the species in a rapidly changing landscape due to human activities.

Ecological niche models (ENMs) generate probabilistic estimates of a species' realized niche by combining presence records with ecological conditions at those locations (Phillips et al. 2006, Colwell and Rangel 2009, Peterson et al. 2011, Araújo and Peterson 2012). ENMs inherently generate estimates of a species' realised niche, rather than of the potential, as they draw upon species' occurrence data, and the associated ecological conditions (Phillips et al. 2006, Araújo and Peterson 2012). When these estimates are projected geographically, the term species distribution model (SDM) is often used (Franklin 2009, Raes and Aguirre-Gutiérrez 2018). Developing ENMs or SDMs for mobile species, such as badgers, presents additional challenges, as consideration of habitat characteristics associated with single sightings or burrow locations can lead to omission of habitat used by animals while ranging (Etherington et al. 2009). In order to estimate the relative importance of environmental conditions required for the persistence of mobile species, it is necessary to incorporate properties of their entire home range. Badger home ranges are, however, highly variable across Europe, with mean size of group territories ranging from 0.14 km^2 in the open habitats of the British Isles (Cheeseman et al. 1981), to 25 km^2 in the continuous woodlands of Poland (Kowalczyk et al. 2003). Here, food abundance and availability is generally recognized as the main determinant of home-range sizes and population densities (Kruuk 1989, Kowalczyk et al. 2000), with low abundance or patchy distribution of food driving larger territories (Kowalczyk et al. 2006).

In the present study, we provide a general framework for estimating habitat suitability in mobile species, which we apply to the European badger occurring in the Netherlands. Specifically, we relate badger sett presence in the Netherlands to environmental drivers using the maximum-entropy algorithm (MaxEnt) for ENM building (Elith et al. 2006, 2011, Phillips et al. 2006, Merow et al. 2013). Environmental drivers, as identified in literature, included land-cover, terrain and groundwater-table variables. To account for landscape properties of the entire home range of individuals, we developed a series of ENMs that include land-cover characteristics at increasing distances around sett locations, using a neighbourhood analysis. We expect model accuracy to be maximum at the spatial scale best representing the home range of badgers in the Netherlands. In accordance with habitat preferences in other central European countries, we expect badger distribution to be strongly influenced by land-cover variables; particularly, the combined presence of grassland and/or maize cropland for feeding and woodland to provide shelter. The outputs of this study result in realistic predictions of habitat suitability for badgers in the Netherlands. The findings provide a useful tool to predict the impact of land-use change on badger populations in this country, as well as to direct future conservation and management decisions. Furthermore, we provide a general framework to estimate habitat suitability for mobile species.

Material and methods

Study area

This study was conducted utilizing geographical data across the entire country of the Netherlands. The Netherlands is a highly engineered, urbanized country, which has resulted in extensive fragmentation of remnant habitats (van der Zee et al. 1992, Dekker and Bekker 2010, Feranec et al. 2010). The country historically experienced dramatic deforestation, which was later partially restored through reforestation of some areas (Daamen 2008), and sustains intense agriculture and livestock farming (Oenema et al. 2005, van Os and Gies 2011).

Badger sett location data

European badger presence in the Netherlands was determined from sett presence records. These were extracted from the Dutch National Database of Flora and Fauna (NDFF; <www.ndff.nl>), which contains records of main badger setts. Most of these records were collected in 2005 by the private nature-conservation organisation Das & Boom, which held a professional and thorough sett survey for the entire country that recorded presence of main badger setts. These data were extended with validated records of (main) setts in the period 2001–2010, which were independently added to the NDFF. All sett locations were recorded at a precision of 1 km^2 (= 100 ha), totalling a number of 1515 unique sett presence records (i.e. an area of 1515 km^2 with presence of a main badger setts) (Fig. 1, black dots). This was

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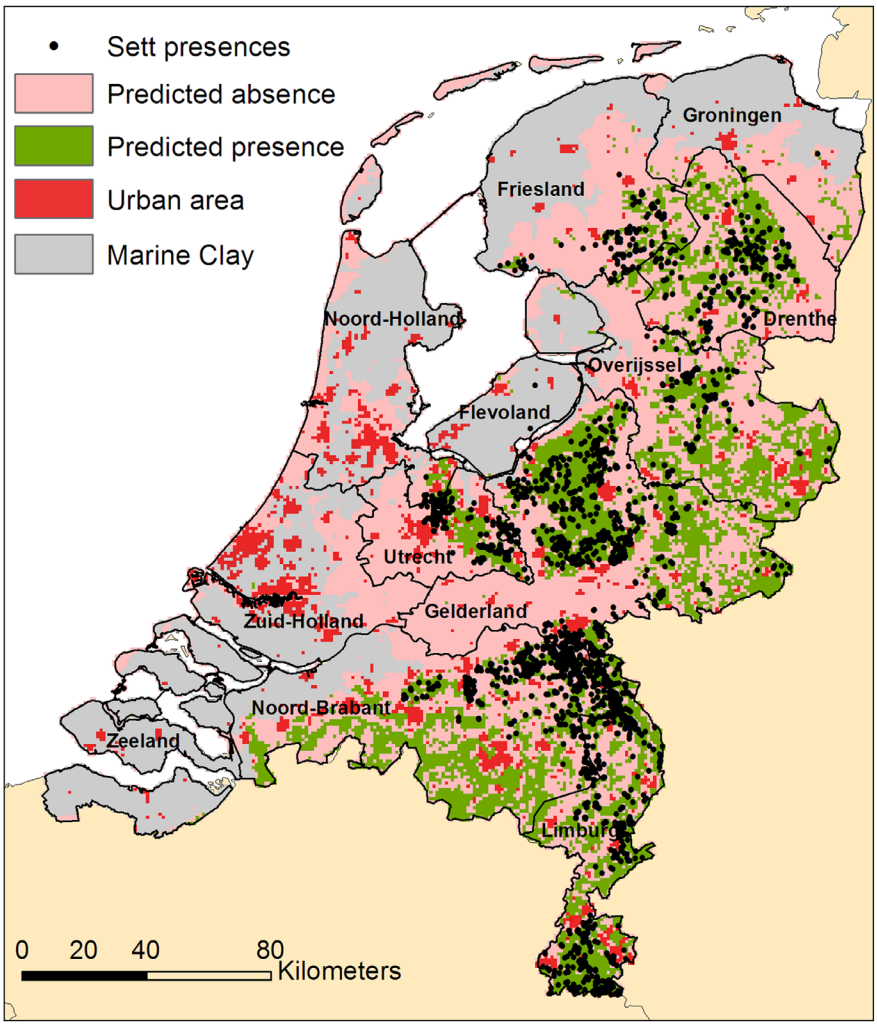


Figure 1. Predicted badger distribution in the Netherlands. Thresholded habitat suitability map for the model using the optimum distance class of 0.5 km outer radius. Black dots indicate badger-sett presences that were used to train the model. Marine-clay areas (grey) were excluded from model parameterization.

more than half the number of estimated setts in the country (approximately 2570 setts in 2001) (van Moll 2002, 2005). The adequacy of our spatial resolution was supported by the study performed by van Apeldoorn et al. (2006), which established that the area used by badgers in the year 2000 ranged between 90 and 115 ha in a local population of badgers in the Netherlands.

Environmental predictors

Thirty-five environmental variables were initially considered to estimate habitat suitability for badgers in the Netherlands. These were selected according to their ecological relevance for badger habitat, based on screening of published literature (Supplementary material Appendix 1 Table A1). The environmental predictors were categorized into six classes: 1) altitude (Jarvis et al. 2008), 2) relief (Jarvis et al. 2008), 3) soil type (Bolsius et al. 1994), 4) groundwater table (Bolsius et al. 1994), 5) openness of the landscape (Meeuwsen and Jochem 2011) and 6) land cover (Hazeu et al. 2010) (Supplementary material Appendix 1 Table A1). All environmental variables were contemporary to badger-sett data (2001–2010) (Supplementary material Appendix 1 Table A1), except for groundwater and soil data, which were from 1990–1995. However, given the temporal stability of such landscape features, these measures remained relevant to our study period. Altitudinal data was obtained from CGIAR-CSI Shuttle Radar Topographic Mission (SRTM) Database (Jarvis et al. 2008), which was measured in 2008 at a spatial resolution of 90 m, and was aggregated to 1 km^2 using the mean value. Relief was expressed as the standard deviation of the mean altitude for each 1 km^2 raster cell, representing terrain heterogeneity. Soil-type and groundwater-table data were collected from the Landschapsecologische Kartering Nederland (LKN) Database (DLO-Staring Centrum 1997) at a spatial resolution of 1 km^2, and were measured over the period of 1990–1995. The original 237 soil classes were reclassified into eight classes by merging them according to similar ecological characteristics (Supplementary material Appendix 1 Table A1). The original twelve classes in the groundwater-table data were also reclassified to six classes in the same way (Supplementary material Appendix 1 Table A1). The openness of the landscape, defined as average viewing

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distance in meters (Meeuwsen and Jochem 2011), was calculated in 2009 by averaging the viewing distance in all directions at each point in the dataset. This was achieved using the computer model ViewScape (Alterra), which uses high-resolution data on topography, land cover and elevation. Landscape-openness measures were obtained at a spatial resolution of 100 m and subsequently aggregated to 1 km^2 using the mean value from 100 cells. Land-cover data were taken from Landelijk Grondgebruiksbestand Nederland (LGN6) (Hazeu et al. 2010), covering the period 2007–2008. These data, developed and used by the Dutch government, included a combination of land-use and land-cover variables (Supplementary material Appendix 1 Table A1). For simplification, we refer to all as land-cover variables. LGN6 distinguishes 39 land-cover classes at a spatial resolution of 25 m^2 for the whole of the Netherlands. Classes with similar ecological characteristics were grouped into a total of 17 classes (Supplementary material Appendix 1 Table A2), resulting in 17 Boolean maps. The Boolean maps were aggregated to 100 m^2 resolution and expressed the percentage coverage of each land-cover class per 100 m^2 raster cell. We applied neighbourhood analyses to land-cover data using 12 distance classes ranging from 0.5–10 km and aggregated the results to 1 km^2 using mean percentage coverage values. Data layers were modified using ArcGIS ver. 10.1 (ESRI), and Python (<www.python.org>, see Supplementary material Appendix 2 for the script used).

To avoid issues associated with multicollinearity and model overfitting, we used Spearman's rank correlation to test for variables' correlation at all distance classes (see neighbourhood analysis below). Only variables with $r_s < 0.7$ were retained, selecting the most ecologically meaningful variable from clusters of correlated variables (Dormann et al. 2013). A table showing how often variables were found to be correlated at the various distance classes is provided in the Supplementary material Appendix 1 Table A3. Furthermore, a table displaying the selection criteria for each pair of correlated variables is provided in Supplementary material Appendix 1 Table A4. Only variables that were not correlated throughout all distance classes were retained, with the exception of land cover class 'woodland' and soil type 'Pleistocene sand' that were marginally correlated ($r_s = 0.703$) at radius' 7.5 and 10 km. These two variables were retained on grounds of their ecological relevance. See Supplementary material Appendix 1 Table A1 for an overview of the excluded variables due to correlation. All correlation analyses were performed in R ver. 3.0.3 (<www.r-project.org>).

Neighbourhood analysis

A neighbourhood analysis was used to determine the importance of different land-cover variables (Table 1) within varying distance classes (i.e. including varying areas surrounding the badger setts). This was to account for potential habitat elements used by badgers while ranging, and not solely the habitat elements present at each sett site (see Etherington et al. 2009 for an analysis using landscape features in a fixed 0.49 km^2 area around badger setts). We only applied neighbourhood analysis to land-cover variables as these dictate resource distribution within badger home ranges, while soil or terrain variables affect suitability for settlement and are therefore only meaningful at sett locations. Therefore, soil type, groundwater table, altitude, relief and openness of the landscape were held constant while land-cover variables varied at the different distance classes during neighbourhood analysis.

Rather than assume a pre-specified home-range size, we performed our neighbourhood analysis using a circular moving window of 12 different radii (here referred to as distance classes) ranging between 0 and 10 km: 0, 0.1, 0.2, 0.3, 0.5, 1.0, 1.5, 2.0, 2.5, 5.0, 7.5 and 10.0 km outside the 1 km^2 raster cells in which setts were located (Fig. 2). These distance classes correspond with home-range areas of 1.0, 1.4, 1.8, 2.4, 3.6, 7.9, 13.5, 19.6, 28.3, 95.0, 201.1 and 346.4 km^2 respectively (Fig. 2). This range extends well beyond the maximum home-range territory known for badgers, estimated at 25 km^2 (Kowalczyk et al. 2003). Model fit on environmental data that includes information beyond the area of badger home ranges should result in lower model accuracy. Therefore, iterative model fitting on data at varying distance classes allows identifying the distance class at which model accuracy is maximum, hence being the best representation of badger home-range area in the Netherlands. The large range of distance classes was used to assess our method, by observing the decrease in model accuracy for spatial scales that exceeded areas used by badgers. See Supplementary material Appendix 2 for the script used for moving-window analyses.

Table 1. Selection of variables used to model badger distribution in the Netherlands sorted according to importance.

Name	Predictor class	Regularized training gain at 0.5 km outer radius of single predictor models
Woodland (%)	land cover	0.239
St. dev. altitude	altitude	0.175
Openness of the landscape	landscape	0.096
Pleistocene sand (%)	soil type	0.085
Urban infrastructure (%)	land cover	0.079
Grassland (%)	land cover	0.059
Periodic high water (wet)	groundwater table	0.055
Clay, other than river and marine clay (in %)	soil type	0.044
Loamy soils (%)	soil type	0.034
Dunes (%)	soil type	0.030
Mostly dry (moist)	groundwater table	0.011
Maize (%)	land cover	0.007
Other crops (%)	land cover	0.003

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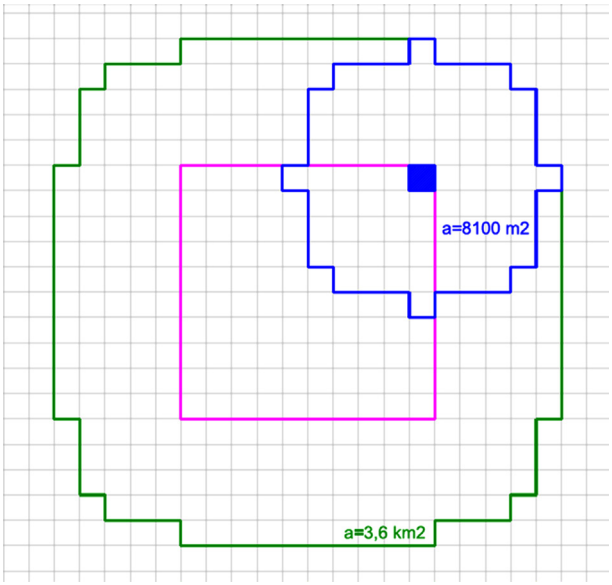


Figure 2. Illustration of the neighbourhood analysis with 0.5 km outer radius (optimum distance class). The moving window shape is outlined in blue, drawing an approximate circular area made of 8100 m^2 cells around the central-blue cell. The environmental data from the blue perimeter is attributed to the central-blue cell using the mean value. The data were aggregated to 1 km^2 by averaging the values of all cells in the pink square, effectively taking into account the area outlined in green covering 3.6 km^2, as the moving window had been previously applied to each cell.

MaxEnt algorithm

Maximum entropy modelling (MaxEnt ver. 3.3.3k, <https://github.com/mrmaxent/Maxent/tree/master/ArchivedReleases/3.3.3k>) was used to identify the spatial distribution of suitable habitat conditions for badgers in the Netherlands, and to estimate the relative importance of environmental factors. MaxEnt is an ecological niche modelling approach developed to utilize presence-only records of target species (Phillips et al. 2004, 2006). MaxEnt is a machine learning method that estimates the species' probability density distribution subjected to environmental constraints using the maximum entropy principle (Jaynes 1982). MaxEnt assigns a value of log-scaled probability of occurrence between 0 and 1 to each raster cell in the study area. This modelling approach was selected given the availability of presence-only data of badger setts. Furthermore, the aim of this study was to identify variables that drive habitat suitability of badgers and, unlike other algorithms, MaxEnt allows for assessment of variable contributions to the final model (Phillips et al. 2004, 2006). Finally, MaxEnt has been shown to outperform other modelling algorithms (Elith et al. 2006, Ortega-Huerta and Peterson 2008, Phillips and Dudík 2008, Aguirre-Gutiérrez et al. 2013, Thibaud et al. 2014). MaxEnt may perform poorly when biased samples are used and bias is unaccounted for (Phillips et al. 2009, Kramer-Schadt et al. 2013, Fourcade et al. 2014). However, sampling bias is a problem only in cases when specific sections of ecospace are not covered (Kadmon et al. 2004, Loiselle et al. 2007, Raes 2012). This was not a concern in our study, given the thorough sampling and the balanced survey design which covered the entire country and the complete potential distribution of the species.

Badger sett locations and selected environmental predictors (Table 1) were used as inputs for MaxEnt models. For each of the 12 distance classes, the models were trained using the 1515 sett presence records, and 10 000 background points. We used MaxEnt's default settings, except, following Merow et al. (2013) we excluded product, threshold and hinge features to avoid model overfitting. Furthermore, we used the recommended maximum sensitivity plus specificity threshold to convert the continuous MaxEnt output to discrete presence and absence predictions for the Netherlands (Liu et al. 2013).

Variable importance

We used a Jackknife test to assess variable importance in predicting badger distribution in the Netherlands. Each Jackknife test consists of two series of models. First, each variable is excluded in turn and a model is created with all remaining variables. The decrease in MaxEnt training gain (a measure of goodness of fit) is compared to the training gain of a model that uses all variables, indicating the importance of the variable to the full model. Second, a model is created using each variable in isolation. The training gain of each of these single-variable models indicates variable's independent importance. Variables' response effects were analysed through the single-variable response curves, showing how the logistic measure of habitat suitability changes along a single gradient (Phillips et al. 2006). These tests were performed for each of the 12 distance classes (i.e. same analyses were performed for each distance class).

Series of MaxEnt runs

The initial model run indicated that badger setts are absent from areas with marine clay (Supplementary material Appendix 1 Table A5, Fig. A1). As such, marine clay was a highly strong predictor of badger absence in the Netherlands. While this was a relevant result, to further assess the contribution of other environmental variables determining habitat suitability in areas where badgers could actually occur (i.e. in areas without marine clay), we masked all areas with marine clay from subsequent analyses. The remaining area studied covered 10 908 km^2 (the Netherlands minus marine-clay areas).

In order to avoid model over-parameterization, we ran a second series of MaxEnt models to identify all variables with very low contribution to the models (regularized training gain < 0.003; See Supplementary material Appendix 1 Table A1 for variables excluded due to low contribution, highlighted in blue). Thereafter, we ran a third and final series of MaxEnt models at all distance classes using the remaining thirteen selected variables (Table 1).

Selection of optimal distance class

We hypothesized that ENM accuracy is at its maximum at the spatial scale that best represents the home range of badgers in the Netherlands, as distance classes below or beyond this should result in lower model accuracy. Optimal ENM

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accuracy was indicated by the model with the highest AUC value, a widely used measure of model accuracy (Elith et al. 2006, Raes and ter Steege 2007, Raes and Aguirre-Gutiérrez 2018). Of available measures, AUC is also the least sensitive to prevalence (Manel et al. 2002, McPherson et al. 2004). This is particularly important when presence-only data are used together with a background sample, given that the latter is generally very large relative to the former, which results in low prevalence (Proosdij et al. 2015). Optimal ENM accuracy allowed identifying the neighbourhood distance that best explained sett presence and habitat suitability in the Netherlands.

Model significance testing

To test the significance of the optimum model we used the null-model test (Raes and ter Steege 2007). The AUC value of the optimum model was tested against a null distribution of 99 AUC values. AUC values were derived from models based on 1515 randomly drawn 'presence data' points from the Netherlands, excluding marine-clay areas (equally many as observed sett locations), replicated 99 times. A significant model (ranked AUC value > 95th null distribution AUC value; $p < 0.05$) would indicate that the relationships between sett presence localities and the explanatory variable values at those locations are significantly stronger than can be expected by chance alone.

Results

All models with different distance classes performed well, with an average AUC value of 0.767 ± 0.05 (Fig. 3). The model with an outer radius of 0.5 km (i.e. the model using a moving window of 0.5 km outer radius in land cover classes) held the highest AUC value of 0.77 (Fig. 3). This moving window resulted in a home range with a diameter of 2 km (extending 0.5 km on all sides of the 1 km² containing the badger sett), and a surface area of 3.1 km² (Fig. 2). The accuracy of this model was significantly better than random expectation when tested against the null-distribution ($p < 0.01$). Therefore, this model best explained the distribution of badgers in the Netherlands. Predictions for all distance classes were consistent, resulting in similar predicted badger distributions (Supplementary material Appendix 1 Fig. A2). Most of the predicted suitable habitat for badgers in the Netherlands coincided with the current distribution of setts in the country. However, some areas with high predicted suitability are currently not colonized, especially in the provinces of Brabant, eastern Gelderland and Overijssel, which were historically inhabited by badgers (Fig. 1).

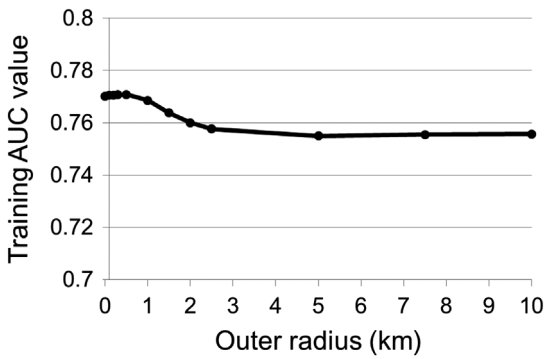


Figure 3. AUC values of habitat suitability models for 11 distance classes representing home range of badgers in the Netherlands.

Different moving window sizes (i.e. spatial scales) resulted in different importance of variables to the models, which is shown by the regularized training gains of models trained on variables in isolation (Fig. 4a). Nonetheless, ranked importance of variables (i.e. importance of variables relative to one another) remained stable until an outer radius of 1.5 km (diameter of 4 km). The shift in variable importance at larger spatial scales is explained by the 'blurring effect', where a larger moving window results in spatial averaged land-cover values of a larger surface area. This results in different land-cover input data to the model, hence changing contributions of variables to the models (Fig. 4a). Regularized training gain using all variables decreased steeply beyond the range of the optimal model with a 0.5 km outer radius (Fig. 4b; red line with black dots). Regularized training gain declined greatest when excluding urban infrastructure, followed by clay

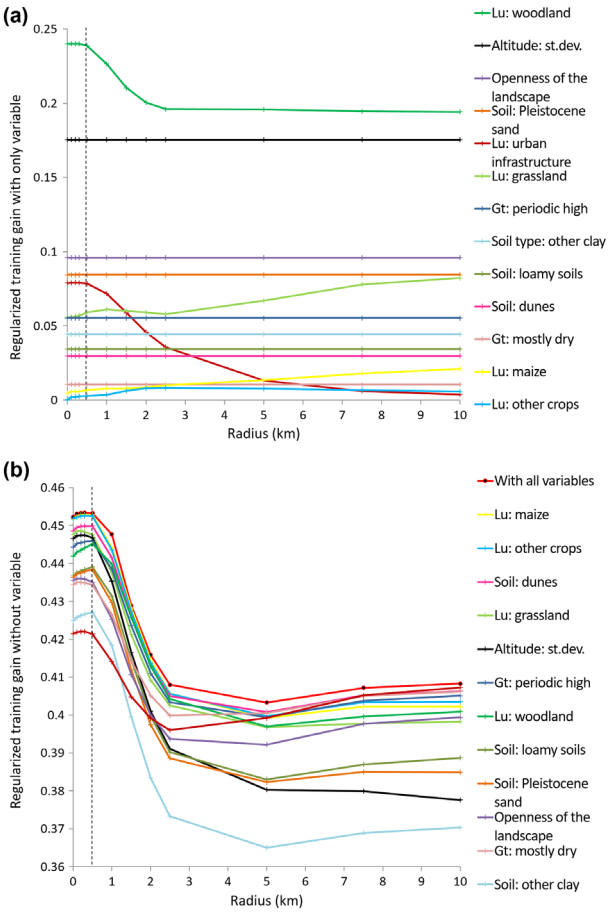


Figure 4. Regularized training gain of variables when modelled in isolation at different distance classes (a) and when excluded from the full model at different distance classes (b). See Table 1 for an explanation of the variables. Note that moving-window analysis was applied to land-cover variables only, while soil and terrain variables were held constant across distance classes.

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soils other than river and marine clay (Fig. 4b), indicating the importance of these variables in determining habitat suitability of badgers. Conversely, omission of woodland did not decrease the training gain considerably (Fig. 4b), but when used in isolation this variable resulted in the highest training gain, therefore, best explaining badger-sett distribution (Fig. 4a).

The response curves for environmental variables at 0.5 km outer radius indicated that a proportion of approximately 60% woodland cover is optimum for badgers (Fig. 5). The density of urban infrastructure had a strong negative effect on badger habitat suitability (Fig. 5). Omission of this variable resulted in the largest decrease in overall model regularized training gain, indicating that urban infrastructure contains useful information that is not contained by the other variables (Fig. 4b). The presence of clay soils other than river and marine clay had a positive effect on badger habitat suitability. Terrain heterogeneity, represented by standard deviation of altitude (i.e. relief) showed an optimum effect on badger habitat suitability at a value of about 17 m km^{-2}. Openness of the landscape and wet soils had strong negative effects on badger sett presence, while Pleistocene sand and loamy soils had positive effects on badger habitat suitability. The presence of grassland and maize crop had limited impact on the distribution of badger habitat (Fig. 4). Both variables yielded optimum conditions at intermediate levels (Fig. 5). Variables' response curves were similar at all distance classes (data not shown).

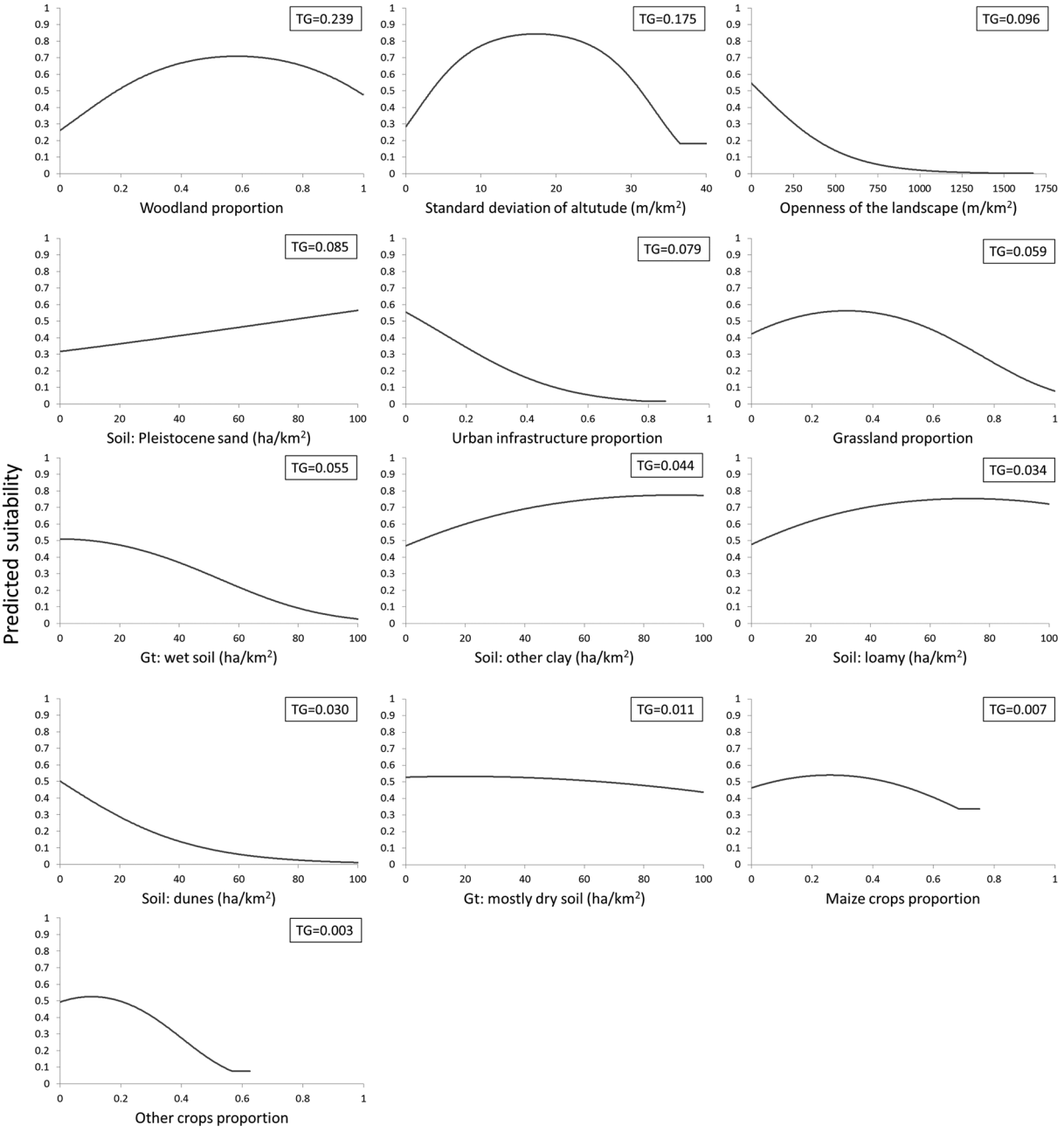


Figure 5. Response curves of explanatory variables of the badger model in the Netherlands at the 0.5 km outer radius (optimum distance class). TG stands for training gain (a measure of goodness of fit).

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Discussion

The environmental factors determining badger habitat distribution in the Netherlands were atypical when compared to previous badger habitat suitability studies in this country (van der Zee et al. 1992, van Apeldoorn et al. 2006). According to our results, the most important drivers are presence of woodland, terrain heterogeneity and openness of the landscape. Grassland and maize crops were not influential habitat elements, which contradicts the current view of the Dutch scientific and conservation community (Westra and Achterberg 2007).

According to our results, the presence of woodland is the main driver of badger distribution in the Netherlands. Woodland is generally related to the provision of refuge and suitable sett sites rather than to the availability of food (Piza-Roca et al. 2014). Here, woodland offers sheltered conditions from human activities as well as structural support for the construction of setts within the root system of trees (Palphramand et al. 2006, Obidziński et al. 2013). Badger preference for woodlands as sett locations has been documented in many other studies (reviewed by Piza-Roca et al. 2014). Moreover, our results indicate that terrain heterogeneity had an optimal effect at intermediate levels, also suggesting a preference for locations that provide shelter. This was further supported by the strong negative effect of landscape openness, a result which is coherent with other studies conducted elsewhere (Thornton 1988, Macdonald et al. 1996, Good et al. 2001, Jepsen et al. 2005). In addition to the provision of shelter, moderate slope might also facilitate sett digging, as excavated soil is likely easily removed on slopes (Neal 1972, Macdonald et al. 1996, Good et al. 2001).

Urban infrastructure had a strong negative effect on badger presence, reflecting the negative impact of anthropogenic disturbance (e.g. lack of shelter and suitable sites for setts) on habitat suitability. This aligns with the findings by Balestrieri et al. (2009), on radio-tracked badgers in northern Italy, and by Silva et al. (2017), in Scotland. While Huck et al. (2008) found that badgers were present in English towns when suitable wasteland and/or woodlands were available within city limits, these conditions are less common in the Netherlands. Lastly, our results suggest an important role of soil type in determining badger sett presence. Marine clay was unsuitable for badger setts, likely because it is too wet and is associated with high water tables, which may inhibit the digging of underground setts. Pleistocene sand, nonmarine or river clay and loamy soils all support the presence of badgers, although their importance appears limited. Generally, dry, well-drained and easily excavated soils, which are found in higher elevation Pleistocene sand formations in the Dutch territory, are associated with badger preferred locations (Skinner et al. 1991, Hammond et al. 2001, Mickevičius 2002).

The observed dependence of badgers on structural elements rather than food sources is not common in central Europe, where current literature points to a strong dependence on factors associated with food availability (reviewed by Piza-Roca et al. 2014)). In central and western Europe, grassland is regarded as a key resource, mainly due to high earthworm abundance, which is a preferred food item (Kruuk and Parish 1981, Lüps et al. 1987, Boyle and Whelan 1990, Kowalczyk et al. 2003, Palphramand et al. 2006, Etherington et al. 2009, Mysłajek et al. 2012, Reid et al. 2012). Also in the Netherlands, grasslands and maize crops are regarded as an important food source for badgers (van Apeldoorn et al. 2006). However, the last study in the Netherlands was performed on a single, isolated population of badgers. When considering the entire Dutch badger population, our results show little to no effect of grassland and maize crops on badger-sett distribution. This may be explained by the country's agricultural landscape, as patches of grassland and maize crops are commonly found in the vicinity of woodlands. At the same time, badgers are opportunistic feeders that take a large variety of animal and plant food sources (Kruuk and Parish 1982, Kruuk 1989, Neal and Cheeseman 1991, Macdonald and Barrett 1993, Martín et al. 1995). Given their highly adaptive diet, badgers do not appear to encounter significant problems in finding food in the Netherlands, while suitable sett-site availability remains a key limiting factor. These results align with studies in southern Europe, where Rosalino et al. (2005) found that suitable sett-site availability, and not food availability, constrained badger distribution.

Our models predict potentially suitable habitat for badgers in areas located in the south (Noord-Brabant) and east (Overijssel and Gelderland) regions of the Netherlands, which are not currently occupied (Fig. 1). Historically, badgers once occupied these regions (van Wijngaarden and van de Peppel 1964), but were actively persecuted and exterminated during the 1960s. This, together with the loss, degradation and fragmentation of habitat, resulted in the disappearance of badgers from large parts of the provinces of Noord-Brabant, Gelderland, Overijssel, Drenthe and Friesland (van Wijngaarden and van de Peppel 1960, van Wijngaarden and van de Peppel 1964, Dirkmaat 1988). Since then, badger population recovery has been relatively slow, with only a few kilometres recolonized every five years (Hollander and La Haye 2014). Given this, the natural recolonization of suitable areas in the southern and eastern regions of the Netherlands could take decades. Landscape isolation related to barriers such as motorways and large rivers may further inhibit natural badger dispersal (Schippers et al. 1996). Our results suggest a high probability of success for recolonization in areas with high habitat suitability.

We found that badger presence was mostly influenced by the landscape composition within an area of 3.6 km^2, as indicated by optimal model accuracy. While all window sizes resulted in good predictive models with high AUC values, model accuracy decreased after an area of 3.6 km^2. The overall high AUC values are the result of the high number of presence points that were available and used to train the models (n = 1515). AUC plateaued for areas larger than 19.6 km^2, suggesting that contribution of land cover variables to model fit ceased after that distance. Stable AUC values beyond this distance reflect the predictive power of soil and terrain variables that were held constant. While an area of 3.6 km^2 best explained badger sett presence in the Netherlands, this may be larger than the actual home-range size of badgers in reality. For instance, if badger setts are not

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located at the centre of the area included in analysis, a larger area would be required to include the totality of the home range.

It should be noted that the smallest area considered in our analyses was 1 km^2, which falls within the range of areas determined by van Apeldoorn et al. (2006) as those generally used by badger groups in a Dutch population. This may imply that the spatial resolution of this study might not allow for determination of sett-site characteristics alone, but more generally for characteristics of the landscape properties of badger home range. Generally, SDM at large scales allows for characterising the target species' Eltonian niche, which is mainly determined by scenopoetic variables, and relevant for understanding the large-scale ecological and geographic species requirements (Elton 1927, Soberón 2007), such was the aim of this study. On the contrary, finer scale modelling, together with mechanistic modelling approaches, allow for the characterisation of the Grinnellian, which is determined by biotic and trophic interactions (Grinnell 1917, Soberón 2007, Peterson et al. 2011). In order to gain further insight into the Grinnellian niche of badgers in the Netherlands, future studies should be performed using finer spatial resolution and detailed knowledge of badgers' home ranges. Moreover, these studies should use badger locations or tracking data, rather than sett locations.

Overall, our results have important implications for badger management strategies in the Netherlands. The environmental factors to target are visual hiding, moderate terrain heterogeneity, urban remoteness and suitable soil conditions for sett digging. Suitable areas need to be large enough, preferably over 3.6 km^2 to accommodate optimal home-range requirements. Future management plans for badgers in the Netherlands should aim at preserving the identified sites with high habitat suitability, or actively modify the landscape to the presented requirements. Additionally, our model provides a tool to predict the effects of future land-use changes on the distribution of badgers. Finally, our approach can be applied to any other mobile species for which sufficient, spatially unbiased presence data are available. We provide a useful methodological framework to realistically model species habitat requirements taking into account the entire home ranges of mobile animals. This may result in important contributions to management and conservation of animal species.

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Supplementary material (available online as Appendix wlb-00453 at <www.wildlifebiology.org/appendix/wlb-00453>). Appendix 1–2.

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