Biodivers Conserv
DOI 10.1007/s10531-017-1333-9

ORIGINAL PAPER

Reintroduced Eurasian beavers (*Castor fiber*): colonization and range expansion across human-dominated landscapes

Kristijn R. R. Swinnen[1,2] · Diederik Strubbe[1] · Erik Matthysen[1] · Herwig Leirs[1]

Received: 30 May 2016 / Revised: 8 March 2017 / Accepted: 12 March 2017

Abstract The protected Eurasian beaver *Castor fiber* is recolonizing its former range hereby entering human-dominated landscapes. This ecosystem engineer can cause considerable damage to human infrastructures and agriculture, by feeding, digging and damming. To prevent human–wildlife conflict and ensure continued support from the local residents, a better understanding of habitat selection is required. By using species distribution models (SDMs) to quantify habitat requirements in our study area in Flanders, Belgium, based on 1792 occurrence data from 71 territories, and a fine-scale land use and vegetation map, we explored the potential for future beaver settlements. The results indicate that even in a highly human-dominated landscape, there is sufficient habitat available to support beaver populations. We highlight the importance of distance to water,

Communicated by Angus Jackson.

Kristijn R.R. Swinnen and Diederik Strubbe are shared first authors.

This article belongs to the Topical Collection: Invasive species.

Electronic supplementary material The online version of this article (doi:10.1007/s10531-017-1333-9) contains supplementary material, which is available to authorized users.

✉ Kristijn R. R. Swinnen
Kristijn_swinnen@hotmail.com

Diederik Strubbe
diederik.strubbe@gmail.com

Erik Matthysen
erik.matthysen@uantwerpen.be

Herwig Leirs
herwig.leirs@uantwerpen.be

1 Evolutionary Ecology Group, Biology Department, University of Antwerp, Campus Drie Eiken, Universiteitsplein 1, 2610 Wilrijk, Belgium

2 Natuurpunt Studie, Natuurpunt, Coxiestraat 11, 2800 Mechelen, Belgium

Published online: 18 March 2017

willow stands, wetland vegetation and poplar trees. We show that there is currently sufficient habitat to support 924 territories (619–1515, 90% confidence interval) in Flanders (but this does not imply these locations are conflict-free). Our findings indicate that 12 year after the reintroduction, there continues to be a large expansion potential, both in range and in densities within the currently recolonized area. Our results can be used as a management tool in order to evaluate possible risks linked with the return of beavers in a human dominated landscape. At these critical locations, increased monitoring or structural measures can prevent conflicts. By preventing or quickly resolving human wildlife conflicts, long-term coexistence between humans and beavers can be achieved.

Keywords Ecosystem engineer · Recolonization · Semi-aquatic mammal · Species distribution model · Species management · Urbanized landscape

Introduction

A major challenge for conservation biology is facilitation of co-existence between humans and wildlife. Human–wildlife conflicts arise when wildlife activities or presence negatively impacts upon humans (Treves et al. 2006). The effects of human–wildlife conflicts can range from agricultural losses by damaging crops (Sitati et al. 2005; Ficetola and Bonardi 2014) to the killing of people (Choudhury 2004). The traditional lethal retaliation against these individuals or species is currently frequently illegal or socially unacceptable (Treves et al. 2006). Human–wildlife conflicts not only arise when an increase in human population and/or expansion of human activities lead to increasing encroachment into wildlife habitats, but can also occur when species which were once highly reduced in numbers, or even locally extinct, recover and expand into human-dominated areas. Conservation management can be especially difficult if such species are protected or endangered while posing a threat to human well-being, as is for example the case for carnivores and elephants. In Europe, large carnivores are recovering (Chapron et al. 2014) and although the acceptance is in general high, predation on livestock and pets can cause conflicts (Kaczensky 1999; Lescureux and Linnell 2014). In Africa and Asia, locally recovering elephant populations (*Loxodonta africana* and *Elephas maximus*) cause an increase in damage on crops, destroying of houses and injuring or killing of people (Zhang and Wang 2003; Sitati et al. 2005).

Human–wildlife conflicts are of increasing conservation concern in Europe, not in the least because over the last decades, stronger environmental protection regulations have allowed several previously (highly) threatened species to recover and recolonize parts of their historical range. Prominent among such species is the Eurasian beaver (*Castor fiber*), a large semi-aquatic rodent, which was nearly driven to worldwide extinction (Nolet and Rosell 1998). Yet, through increased protection, reintroduction projects and natural range expansion, beavers have succeeded in recolonizing most of their natural range (Halley et al. 2012). Eurasian beavers are strictly protected by European law and are listed in the Habitat Directive Annex IV, prohibiting capturing, killing or disturbing them unless when authorised through formal derogation procedures (Pillai and Heptinstall 2012; Vlaamse Regering 2015). Beavers are ecosystem engineers (Jones et al. 1994), controlling availability of resources by causing physical changes in the abiotic and biotic environment (Jones et al. 1997). They can increase species richness on landscape scale (Wright et al.

2002) and are appreciated for their role in restoring waterways and wetland situations (Rosell et al. 2005). Beavers can alter the ecosystem by digging in waterway banks and through the creation of food channels (Hood and Larson 2014) and although dam building is their best known type of habitat modification, this is no requirement for beaver settlement (Hartman and Tornlov 2006, unpubl. data K.S.). Beaver dams cause an increase in water levels and have an effect on hydrology and sedimentation patterns (Nyssen et al. 2011; De Visscher et al. 2014) and also impact upon plant, invertebrate and vertebrate populations/communities (Collen and Gibson 2001; Rosell et al. 2005; Dalbeck et al. 2007; Nummi and Hahtola 2008; Nummi et al. 2011; Nummi and Holopainen 2014). Inundation due to beaver dams is considered to be the main cause of human–beaver conflicts (Taylor and Singleton 2014), but also the destabilisation of banks by digging and the feeding on agricultural crops and fruit/production trees can cause local conflicts (Verbeylen 2003; Kloskowski 2011).

Although studies to understand habitat suitability and selection of Eurasian beavers have been performed (Nolet and Rosell 1994; Hartman 1996; Fustec et al. 2001; Maringer and Slotta-Bachmayr 2006; John and Kostkan 2009; Pinto et al. 2009; John et al. 2010) large scale predictions aiming to investigate future distribution of beavers across landscapes which are currently being colonized are rare, use coarse spatial scales and are mostly based on expert opinion. Macdonald et al. (1995) applied geographical information systems (GIS) to select possible habitat types based on criteria derived from the literature. Another study combined expert opinion and proximity to waterways to assess carrying capacity of parts of Scotland to identify suitable release sites (South et al. 2000; Macdonald et al. 2000). Here, beaver habitat selection in Flanders (Belgium), where beavers were extirpated in 1848 and (illegally) reintroduced in 2003 (Verbeylen 2003), was assessed by means of species distribution models (SDMs).

Since the reintroduction, the beaver population in Flanders has grown continuously, and currently, around 120 territories are occupied (unpubl. data K.S.). Given the relatively recent return of beavers, conflicts are rather limited although the construction of beaver dams, feeding on economically valuable trees and trees very close to houses, and potential destabilisation of waterway banks all have occurred in several territories and frequently needed human intervention. The rate of conflicts is expected to increase later in the colonization process (around 20 years after reintroduction) when population densities increase (Halley and Rosell 2002). The availability of detailed, fine-scale area-wide vegetation and land-use maps allows us to assess beaver habitat selection in more detail than has been done before, and enables us to formulate detailed predictions of areas which are expected to be colonized by re-introduced beavers. We discuss how such detailed predictions will allow to develop adaptive management strategies for returning ecosystem engineers in one of the most densely human populated areas in Europe.

Materials and methods

Study area and species history

This study was conducted in Flanders, the Northern part of Belgium (13,522 km^2). Flanders is densely populated (average human population density of 462/km, Statbel 2010) and is characterised by a number of river valleys with moderate slopes and minor elevation differences (Deckers et al. 2010). Agriculture comprises 58% of the area, residential areas

17% and nature (protected and unprotected) accounts for about 9% (Departement Ruimte Vlaanderen 2013). Most of Flanders' waterways belong to either the Scheldt or the Meuse watershed. The last beaver was exterminated in 1848 but beavers reappeared starting from 2000 after an unofficial reintroduction in Wallonia, the south of Belgium, followed by an unofficial reintroduction of 20 beavers south of Leuven in 2003, in the Dijle and Laan river, both part of the Scheldt watershed (Verbeylen 2003). An additional 22 beavers were simultaneously released in the east of Flanders, near the river Meuse (unpubl. data K.S.). Beaver territories are located in nature reserves, but also in agricultural and even residential areas and water bodies used for recreation (e.g., fishing, walking, wind/kite surfing) and industrial activity (Swinnen et al. 2015).

Occurrence data

Occurrence data were gathered from a range of sources during the years 2011–2014. Beaver territories were reported by a network of local volunteers, by the general public using a citizen-science nature observation data portal (www.waarnemingen.be), by governmental employees responsible for rat control near waterways and by the beaver workgroup, a non-governmental volunteer organisation. Reported locations were visited by K. Swinnen, and by using the criteria described by Dewas et al. (2012), presence of a territory was confirmed or refuted. When in doubt, territory boundaries between neighbouring territories were situated between two consecutive signs with the largest distance between them, as described by Fustec et al. (2001). In total, 1792 beaver occurrences were gathered and locations were entered in a hand held Garmin C60 GPS, corresponding to 71 territories (observations per territory, mean and standard deviation: 25.2 ± 19.6, range 1–66). Although beavers are nocturnal, signs of presence, such as the cutting of trees, are very clear and cannot be confused with other species. Given these conspicuous signs, our elaborate observer network and the high human presence throughout the region, we expect almost all territories to be included. Furthermore, to reduce the effect of possible spatial sampling bias (Yoccoz et al. 2001), spatial thinning was applied to remove records closer than a minimum nearest neighbour distance, balancing bias removal and signal weakening, using the spThin R package (Aiello-Lammens et al. 2015). This procedure was carried out separately for each territory, and the final dataset used for distribution modelling consisted of 899 occurrences (observations per territory, mean and standard deviation: 9.5 ± 5.8, range 1–17).

Environmental variables

A set of eight habitat and land-use variables were selected based on ecological knowledge about beaver habitat requirements. Beavers are general herbivores, feeding on bark, shoots and leaves of woody plants, and on non-woody plants such as ferns, forbs and aquatic vegetation (Haarberg and Rosell 2006; Krojerová-Prokešová et al. 2010). Studies from the Netherlands and Norway show that European beavers have a strong preference for broadleaved deciduous habitats and mainly consume deciduous trees (Nolet et al. 1994; Campbell et al. 2005). Relevant habitat variables were extracted from the biological valuation map (BVM, version 2.0, Wils et al. 2006), the most recent map available at the time of the modelling, which is a highly detailed standardized survey of the biotic environment, based on vegetation, land use and small landscape elements. Because the BVM has more than 1100 unique vegetation/land-use classes, these were summarized into seven predictor variables relevant to beaver ecology. Three forested habitat types [Willow (*Salix* sp.), Poplar (*Populus* sp.), other deciduous forest]; one shrub-like category: [mainly Hawthorn (*Crataegus* sp.) and Common broom (*Cytisus scoparius*)], two non-woody vegetation types [grassland and wetland vegetation (mainly (*Phragmites australis*) and (*Filipendula ulmaria*))] and semi-natural environments (parks, cemeteries, etc.). Agricultural crops were not considered since they are frequently rotated over the years. Because of this rotation, and the short time window in which crops are favoured by beavers, we expect them to have a limited effect on year-round settlement of beavers. Distance from the nearest water was included as an eighth variable. All water bodies in the BVM were selected and merged with a GIS database characterizing all streams and waterways in Flanders, thereby capturing all aquatic habitats potentially available to colonizing beavers. The Albert Canal, an artificial shipping connection was not considered as a potential habitat as its perpendicular concrete walls do not allow beavers to settle next to the canal (they are unable to exit the canal, and frequently drown, unpubl. data K.S.). Beavers are central place foragers, and large parts of their diet is obtained by moving out of the water to select and cut trees, which are then transported to the water for eating or storing (Haarberg and Rosell 2006). Consequently, beavers prefer to forage close to water, within the riparian zone, and mostly remain within 10–50 m from waterways (Macdonald et al. 1995; Schley 2004; Jones et al. 2009). Therefore, here, waterways were buffered with 50 m and only habitats within these buffers were considered as predictors of beaver settlement.

Environmental predictors were prepared at a cell size of 10 m (a smaller resolution was not realistic given the spatial accuracy of the BVM land-use database). For each of the seven habitat variables, distance grids were created (higher values indicate areas further away from habitat features). For river banks, an 'in-and-out' distance grid whereby negative values represent locations within waterways and locations outside waterways (i.e. on the land) have positive values was calculated.

Species distribution modelling

Species distribution models (SDMs) are statistical techniques to correlate species occurrences with spatial environmental information to estimate the distribution of a species across landscapes (Elith and Leathwick 2009; Guisan et al. 2013). SDMs are applied to a wide range of questions in conservation biology, such as providing information for managing threatened species, to determine the effects of climate change on species distributions and to assess the potential of invasive species (Guisan and Thuiller 2005; Elith et al. 2011; Guillera-Arroita et al. 2015).

To model the potential distribution of beaver in Flanders, the MaxEnt algorithm was used (Phillips et al. 2006) because of its generally high predictive accuracy (Elith et al. 2006; Phillips and Dudík 2008) and common use in biogeography (Elith and Leathwick 2009). Recent studies have pointed out that SDM performance is influenced by model specifications (Anderson and Gonzalez 2011; Radosavljevic and Anderson 2014), and that species-specific tuning of model settings and the use of spatially independent calibration and evaluation datasets may allow for increased model transferability (Anderson and Gonzalez 2011; Radosavljevic and Anderson 2014). Also, MaxEnt models are typically evaluated using the much criticized AUC (Lobo et al. 2014), a model evaluation statistic ranging from 0.5 to 1 (higher values indicate better models). Therefore, in this study, we did not rely on MaxEnt default settings but assessed MaxEnt model performance across a range of model settings using the R package ENMevals (Muscarella et al. 2014). Settings were specified as follows. (1) Four different methods were used to partition the available beaver occurrence data into calibration and evaluation datasets. First, the default 'random

10-fold' cross-validation was used, randomly partitioning occurrence data across bins. Second, the 'block' method, which partitions occurrence data according to the latitude and longitude lines dividing the occurrence data into four bins of (as far as possible) equal numbers, was used. Lastly, two 'checkerboard' partitioning methods were implemented, whereby occurrence data are divided according to checkerboard-like grids (the first checkerboard method applies a single grid to partition occurrence localities in two bins, the second checkerboard adds a second level of spatial aggregation, see Muscarella et al. (2014) for method details. (2) MaxEnt carries out various transformations of the original predictor variables (called 'feature classes', Phillips et al. 2006) to model the relationship between habitat conditions at locations where the species was recorded versus 'background' locations (see below). Distribution models were evaluated along the full range of transformations available (LQHPT; where *L* linear, *Q* quadratic, *H* hinge, *P* product and *T* threshold, Elith et al. 2011; Muscarella et al. 2014). (3) MaxEnt applies a 'regularization multiplier' parameter that controls how closely the model fits the available occurrence data. Following extensive empirical testing, this value has been fixed at a value of 1 (Phillips and Dudík 2008). Here, MaxEnt models were evaluated with a regularization multiplier varying from 0.5 to 5, using 0.5 intervals. Higher values for this multiplier result in stronger 'smoothing' and thus less complex models (Muscarella et al. 2014). (4) Lastly, following (Warren and Seifert 2011), MaxEnt model selection was based on the AIC_C (Aikaike Information Criteria for small sample sizes, Anderson 2008). AICc trades off explanatory power versus model complexity and AIC_C model selection has been shown to result in more robust and transferable SDMs (Elith et al. 2010; Warren and Seifert 2011). Model performance of the best MaxEnt model (i.e. the model with the lowest AIC_C value) was additionally assessed using the Boyce-index, an evaluation statistic specifically designed for presence-only models (−1 to 1, higher values indicate better models, Hirzel et al. 2006).

As background areas should reflect the set of areas a species could potentially have colonized since its presence in the region (Barve et al. 2011), the background area was selected as a minimum convex polygon encompassing all currently established beaver territories (Fig. 1). MaxEnt models were created based on this area and the best MaxEnt model was then projected onto the whole of Flanders to obtain an area-wide prediction of beaver habitat suitability. This resulted in a continuous value between 0 and 1 for every pixel within 50 m of a waterway or waterbody. To convert these continuous predictions into predictions of suitable versus unsuitable pixels, a threshold of the mean habitat suitability value of currently established beaver territories was applied, classifying each pixel as 1 suitable or 0 unsuitable. We never observed that the pixel closest to the water was unsuitable and pixels more inland were suitable. To account for the fact that further away from the introduction site, beavers may not yet be in equilibrium with the environment (Václavík and Meentemeyer 2012), these thresholds were calculated on the area where beavers were first introduced (the Dijle valley, n = 17 territories, see Fig. 1; but note that alternative thresholds were tested on the whole colonized range as well, see below).

To obtain a realistic estimate of the areas which potentially could be colonized by beavers, the minimum amount of suitable habitat to support at least one family territory was estimated. The presence-absence map obtained above served as input for designating discrete habitat patches. First, pixels predicted as suitable that are too far removed from other suitable areas are unlikely to represent relevant habitat patches for colonizing beavers. Beavers do not necessarily need contiguous blocks of suitable habitat. In the Netherlands, territories contained a minimum of 2 km of wooded bank within a maximum of 11 km bank length (Nolet and Rosell 1994). Also in our study area, a number of territories seem to be made up of several smaller blocks of suitable habitat, interspersed with stretches of less suitable river banks (e.g., mainly meadows, unpubl. data K.S.). Therefore, all pixels predicted as suitable and no more than 100 m apart were grouped into a 'patch'. Second, in order to quantify the amount of suitable pixels needed for allowing the establishment of a beaver territory, a minimum convex polygon encompassing all beaver occurrences was created for each territory in the Dijle Valley separately, and then the number of suitable pixels covered by the polygon was extracted. This number of suitable pixels was subsequently applied as a threshold to identify habitat patches large enough to hold at least one beaver territory (note that both the average number of pixels, as the 90% confidence intervals, to bound the uncertainty was used). All statistical analyses were performed in R (Version 3.1.2, the R Foundation for Statistical Computing, Vienna, Austria).

Results

The MaxEnt model with the lowest AIC_C value was obtained using the 'block' data partitioning method, and employed the full range of predictor variable transformations available ('LQHPT', Muscarella et al. 2014) and a regularization multiplier of 3.5. The Boyce-index of this model was 0.82. For comparability with other studies, we also report the AUC based on the evaluation data ('AUC_{TEST}'), which was equal to 0.98.

The most important variable underlying beaver habitat suitability is distance to river banks (variable contribution 48.4), followed by distance to willow trees (28.8) and wetland vegetation (11.6). Distance to poplar trees exerted some influence on beaver habitat suitability (5.7). The remaining variables only marginally contributed to model predictions (all variable contributions <2.2). Habitat suitability was lower further away from river banks. Beaver presence is thus predicted to be high in areas in close proximity to patches of willow and poplar trees in combination with wetland vegetation.

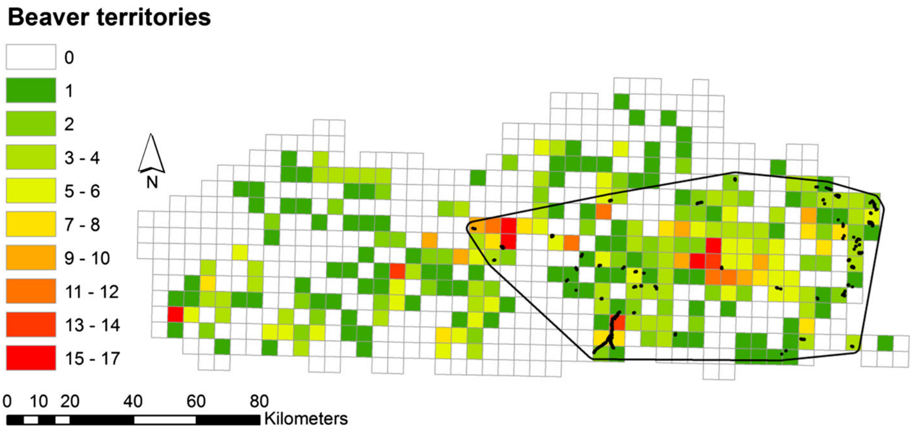

Fig. 1 Region-wide prediction of beaver territories. Number of territories per 5 × 5 km UTM grid was obtained by summing the number of predicted beaver territories within each grid cell. The *black polygon* indicates the colonized area used for building the MaxEnt model. *Black dots* indicate occupied beaver territories by the end of 2014

The mean habitat suitability of currently established territories in the Dijle valley was 0.54 (90% confidence interval 0.51–0.57). Two alternative threshold criteria (calculated on the whole colonized area), based on the Boyce-index and on the true skill statistic (TSS; Allouche 2006) were also applied. These alternative threshold methods resulted in similar cut-off values (0.55 and 0.58, respectively), and we further only considered the Dijle mean habitat suitability. Using this threshold to discriminate between suitable and unsuitable pixels, the Dijle valley beaver territories had on average 304 suitable pixels (90% confidence interval 209–399). Applying these thresholds to predicted beaver suitability across Flanders indicates that across the region, there is sufficient habitat to ecologically support 924 beaver territories (90% confidence interval 619–1515). In order to obtain a clear visual representation of predicted beaver territory establishment, the country was divided in 5 $\times$ 5 km Universal Transverse Mercator (UTM) squares and the number of beaver territories per UTM grid cell was calculated (Fig. 1).

Discussion

Beaver habitat characteristics in a human-dominated landscape

As could be expected, our findings confirm that beaver habitat suitability declines strongly further away from river banks. This corresponds with the findings of other studies showing that beavers preferably forage close to the water, with average maximum reported foraging distances ranging up to 50 m (Macdonald et al. 1995; Jones et al. 2009), but mostly closer (Schley 2004; Iason et al. 2014). The importance of willow for beavers was already reported frequently in other studies. Beavers feed primarily on Salicaceae (Fustec et al. 2001; Jones et al. 2003; Haarberg and Rosell 2006) and willow is the most preferentially eaten species during winter, but is also frequently used during the growing season (Krojerová-Prokešová et al. 2010). Non-woody plants can represent 25–90% of the diet during the vegetative season (Krojerová-Prokešová et al. 2010). We show that distance to wetland vegetation plays an important role in the habitat suitability for beavers. We suspect that this vegetation category represents a general suitability where foraging for various non-woody plants is possible. Furthermore, although reed is not foraged on by beavers (Willby et al. 2011) we frequently noted foraging on young willow shoots present in reed beds (which are classified as wetland vegetation) (unpubl. data K.S.). Poplar trees have already been reported as an important food source for Eurasian (Fustec et al. 2001) and North American beavers (Beck et al. 2010). Most poplar plantations in Flanders were planted several decades ago, resulting in large, thick trees which are less preferred by beavers (Haarberg and Rosell 2006), resulting in a low effect on beaver habitat suitability. Shrubs and grasslands were not important contributors to the model in contrast with findings of Hartman (1996).

Both average density of territories and territory size fall well within reported ranges. The prediction of 924 (619–1515) territories within Flanders corresponds to a density of 0.06 (0.05–0.11) territories/km^2. This is more than the 0.005–0.01 territory/km^2 predicted for Scotland (predictive modelling, South et al. 2000) but less than densities reported in other European countries: Finland, (0.08 territory/km^2, Hyvönen and Nummi 2008) and Lithuania (0.41 territory/km^2, Ulevičius et al. 2011). Size of beaver territories is typically about 3 km (river bank length) but can range from 0.5 to 12.8 km (Macdonald et al. 1995). Nolet and Rosell (1994) showed that territories consist on average of 3 $\pm$ 0.4 km of wooded river bank, highly similar to our finding of 304 suitable pixels per territory (corresponding to 3040 m river bank) for beaver territories in the area near carrying capacity.

Model limitations

In general, our findings correspond with habitat and species diet preferences from other study areas. Because highly detailed vegetation data was available, we chose to calibrate the model based on available vegetation resources and not on parameters indirectly linked and correlated with vegetation such as soil type or stream tortuosity (difference between the length of shore line and the straight line from the one end of the territory to the other) (Hartman 1996; Pinto et al. 2009). Pinto et al. (2009) reported a preference for shallow water, possibly as a consequence of preferred feeding in shallower water. Landscape wide data concerning water depth and bank gradient are unavailable for our study area. Since the majority of waterways are small low order streams, we do not expect that the inclusion of water depth will profoundly alter the territory predictions. Bank gradient is expected to have a limited effect on the overall suitability for territory settlement, although it can influence lodge-site selection (Dieter and McCabe 1989). Stream gradient was not included since Flanders is characterized by minor elevation differences.

Although validation statistics indicate a very good model quality, results should be interpreted with care. Beavers continue to colonize Flanders, and models based on occurrence data inherently model a species' realised niche only (Václavík and Meentemeyer 2012). It is known that dispersing beavers do occupy distant areas earlier than those closer to the previously occupied sites (Hartman 1995; Fustec et al. 2001), indicating they behave as specialists in the beginning of the colonization process, but become more generalists when the population expands (Fustec et al. 2001; Václavík and Meentemeyer 2012). Such a process is a known limitation of correlative distribution models. Yet, we argue at least for Flanders, our models represent a reasonable approximation of the areas likely to be colonized, because (a) since their reintroduction in 2003, beavers have already traversed a large part of our study area, settling in a range of habitats. While it cannot be excluded that they will occupy different habitats in the future, based on the species ecology in neighbouring countries, it seems unlikely beavers would start inhabiting habitats that are very different from the ones in which they currently have (at least some) presence. Moreover, (b) our model selection process led us to base our predictions of range expansion on a model with a relatively high smoothing factor obtained through block data partitioning. Such a higher smoothing forces the model to focus on main trends instead of overfitting local patterns of habitat selection. Building 'smoother' models evaluated through block data partition has previously been suggested as the most robust manner to deal with range-shifting species (Elith et al. 2010; Muscarella et al. 2014), suggesting our current model is as reliable as data currently allow. Apart from estimating habitat suitability, our predictions also depend on the estimated amount of suitable habitat that needs to be present to allow the establishment of a beaver territory. Here, this estimate was based on beaver territories in the Dijle Valley, where beavers were first introduced and where the population likely has reached carrying capacity (beaver territories comprise the whole Dijle and Laan river with rarely an unoccupied stretch of stream between territories). Our estimate is thus likely close to the minimum amount of suitable habitat needed to support a beaver territory. If any factor not directly accounted for in our model would cause beavers to need a significantly larger amount of suitable habitats for establishing a territory elsewhere, the predicted number of beaver territories presented here will be an overestimation.

On the other hand, if the carrying capacity of the Dijle Valley is not yet reached, and beavers will occupy currently unoccupied habitat only at carrying capacity, the predicted number of territories presented here will be an underestimated. As the size of the beaver territories found here correlate with estimates of territory sizes in other areas across Europe, we argue that such a strong over- or underestimation is unlikely. For risk assessment of colonizing, re-introduced species, underestimating a species' potential range and abundance is considered a greater risk than overestimating (see Jiménez-Valverde et al. 2011). Therefore, and given the fact that we, to the extent possible, account for different habitat selection criteria beavers may use during the colonization process, we argue that our results are relevant for environmental management and do constitute a reasonable representation for the continuing recolonization of Flanders by this charismatic species.

Beavers are known as ecosystem engineers which can potentially greatly transform deciduous forest habitats within years. However, most habitats were mapped for the BVM before beavers settled. This means that the habitat variables on the map represent the original habitat situation and we consequently observed what habitat combinations were able to support permanent beaver settlement. Whether or not beavers first needed to modify the habitat does not change the outcome of the model. Depletion of preferred food species is possible (Nolet et al. 1994) but often, these preferred species regrow and depletion is additionally avoided by foraging on aquatic vegetation and occupying large territories, consequently reducing foraging pressure (Campbell et al. 2005; Jones et al. 2009; Pinto et al. 2009). Furthermore, our model indicates the locations that are suitable for beavers, but there is no connectivity included, therefore some of these locations may be unlikely to be reached by beavers. In general, it is assumed that when beavers are present within a watershed they will colonize the watershed (Halley and Rosell 2002) but manmade obstacles can have a clear barrier effect (Halley et al. 2012). In Flanders, the Albert Canal can prevent dispersal as beavers cannot exit the canal and frequently drown. Another possible dispersal barrier are long underground canalisations.

Management implications

The Flemish ministry of environment declares in their species protection act for the beaver (Vlaamse Regering 2015) to aim for 167 beaver territories. Our results indicate that the habitat potential is clearly present and population size will exceed this goal unless population restrictive management measures are taken. Certainly in a highly human-dominated region, damage to agriculture, industry and private properties by foraging, digging or damming is likely. Since most damage occurs close to the water's edge, restoration of a 20 m wide zone of natural vegetation on each bank of the waterway is probably the most durable solution (Nolet and Rosell 1998), but not very realistic in a highly urbanised landscape such as Flanders. In order to maintain the public support for the returning beavers, it is important to anticipate the arrival by informing local stakeholders. Our results can be used to prioritize regions for information campaigns and management actions. Landowners near waterways with high beaver potential can be informed, explaining how to recognise beaver signs, and which mitigation measures can be taken to prevent damage to their properties. Our results can be combined with agricultural and forestry maps in order to delineate potential risk areas for foraging damage. Damage by foraging on crops and production trees can be prevented by fencing parcels or individual trees. Furthermore, increased monitoring for signs of beavers around zones with weak river banks, and reinforcing these with mesh wire to prevent digging can be executed (Niewold 2007). Removal of Willow stands from alongside canals and waterways, where damage by digging could have major effects on structural safety of the banks, could prevent beavers from settling in these areas (Gurnell et al. 2009). Dam sensitive locations (Hartman and Tornlov 2006) can be monitored more frequently, deepened, or when dams are already constructed, a flow device (a pipe trough the dam) can be deployed to lower water to an acceptable depth for both beavers and humans (Taylor and Singleton 2014). Correct measures are very important to reduce or quickly resolve human–beaver conflicts, since the long term fate of the beaver population in Flanders depends on their ability to coexist with humans.

Conclusion

Our results show that even in a highly modified landscape with high human densities, there continues to be a large expansion potential, both in range and in densities within the currently recolonized area, for a returning medium sized semi-aquatic mammal, the beaver.

Acknowledgements K.R.R.S. held a Ph.D. Grant from the Agency for Innovation by Science and Technology (IWT), Flanders, Belgium. We thank all landowners for permission to enter beaver territories. We specifically thank our local volunteers, nature organisations, Natuurpunt and the contributors to www.waarnemingen.be, governmental employees responsible for rat control and the beaver workgroup, a non-governmental volunteer organisation for information considering beaver territories.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Aiello-Lammens ME, Boria RA, Radosavljevic A et al (2015) spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. Ecography (Cop) 38:541–545. doi:10.1111/ecog.01132

Allouche O, Tsoar A, Kadmon R (2006) Assessing the accuracy of species distribution models: prevalence, kappa and the true skill statistic (TSS). J Appl Ecol 43:1223–1232. doi:10.1111/j.1365-2664.2006.01214.x

Anderson DR (2008) Model based inference in the life-sciences: a primer on evidence. Springer, New York

Anderson RP, Gonzalez I (2011) Species-specific tuning increases robustness to sampling bias in models of species distributions: an implementation with Maxent. Ecol Model 222:2796–2811. doi:10.1016/j.ecolmodel.2011.04.011

Barve N, Barve V, Jiménez-Valverde A et al (2011) The crucial role of the accessible area in ecological niche modeling and species distribution modeling. Ecol Model 222:1810–1819. doi:10.1016/j.ecolmodel.2011.02.011

Beck JL, Dauwalter DC, Gerow KG, Hayward GD (2010) Design to monitor trend in abundance and presence of American beaver (*Castor canadensis*) at the national forest scale. Environ Monit Assess 164:463–479. doi:10.1007/s10661-009-0907-8

Campbell RD, Rosell F, Nolet BA, Dijkstra VAA (2005) Territory and group sizes in Eurasian beavers (*Castor fiber*): echoes of settlement and reproduction? Behav Ecol Sociobiol 58:597–607. doi:10.1007/s00265-005-0942-6

Chapron G, Kaczensky P, Linnell JDC et al (2014) Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346(80):1517–1519. doi:10.1126/science.1257553

Choudhury A (2004) Human–elephant conflicts in northeast India. Hum Dimens Wildl 9:261–270. doi:10.1080/10871200490505693

Collen P, Gibson RJ (2001) The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish—a review. Rev Fish Biol Fish 10:439–461. doi:10.1023/A:1012262217012

Dalbeck L, Lüscher B, Ohlhoff D (2007) Beaver ponds as habitat of amphibian communities in a central European highland. Amphibia-Reptilia 28:493–501. doi:10.1163/156853807782152561

De Visscher M, Nyssen J, Pontzeele J et al (2014) Spatio-temporal sedimentation patterns in beaver ponds along the Chevral river, Ardennes, Belgium. Hydrol Process 28:1602–1615. doi:10.1002/hyp

Deckers P, Kellens W, Reyns J et al (2010) A GIS for flood risk management in Flanders. In: Showalter PS, Lu Y (eds) Geospatial techniques in urban hazard and disaster analysis. Springer, Netherlands, pp 51–69

Departement Ruimte Vlaanderen (2013) Overzicht van de evolutie van de ruimteboekhouding van het RSV, gebaseerd op volledig afgeronde planningsprocessen (in Ha)

Dewas M, Herr J, Schley L et al (2012) Recovery and status of native and introduced beavers *Castor fiber* and *Castor canadensis* in France and neighbouring countries. Mamm Rev 42:144–165. doi:10.1111/j.1365-2907.2011.00196.x

Dieter CD, McCabe TR (1989) Factors influencing beaver lodge-site selection on a prairie river. Am Midl Nat 122:408–411

Elith J, Leathwick JR (2009) Species distribution models: ecological explanation and prediction across space and time. Annu Rev Ecol Evol Syst 40:677–697. doi:10.1146/annurev.ecolsys.110308.120159

Elith J, Graham CH, Anderson RP et al (2006) Novel methods improve prediction of species' distributions from occurrence data. Ecography (Cop) 29:129–151. doi:10.1111/j.2006.0906-7590.04596.x

Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. Methods Ecol Evol 1:330–342. doi:10.1111/j.2041-210X.2010.00036.x

Elith J, Phillips SJ, Hastie T et al (2011) A statistical explanation of MaxEnt for ecologists. Divers Distrib 17:43–57. doi:10.1111/j.1472-4642.2010.00725.x

Ficetola G, Bonardi A (2014) Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. Curr Zool 60:170–179. doi:10.1111/j.1472-4642.2007.00377.x

Fustec J, Lode T, Le Jacques D, Cormier JP (2001) Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. Freshw Biol 46:1361–1371. doi:10.1046/j.1365-2427.2001.00756.x

Guillera-Arroita G, Lahoz-Monfort J, Elith J et al (2015) Is my species distribution model fit for purpose? Matching data and models to applications. Glob Ecol Biogeogr. doi:10.1111/geb.12268

Guisan A, Thuiller W (2005) Predicting species distribution: offering more than simple habitat models. Ecol Lett 8:993–1009. doi:10.1111/j.1461-0248.2005.00792.x

Guisan A, Tingley R, Baumgartner JB et al (2013) Predicting species distributions for conservation decisions. Ecol Lett 16:1424–1435. doi:10.1111/ele.12189

Gurnell J, Gurnell AM, Demeritt D, et al (2009) The feasibility and acceptability of reintroducing the European beaver to England. Natural England Commissioned Report NECR002, 1-106

Haarberg O, Rosell F (2006) Selective foraging on woody plant species by the Eurasian beaver (*Castor fiber*) in Telemark, Norway. J Zool 270:201–208. doi:10.1111/j.1469-7998.2006.00142.x

Halley DJ, Rosell F (2002) The beaver's reconquest of Eurasia: status, population development and management of a conservation success. Mamm Rev 32:153–178. doi:10.1046/j.1365-2907.2002.00106.x

Halley D, Rosell F, Saveljev A (2012) Population and distribution of Eurasian beaver (*Castor fiber*). Balt For 18:168–175

Hartman G (1995) Patterns of spread of a reintroduced beaver *Castor fiber* population in sweden. Wildl Biol 1:97–103

Hartman G (1996) Habitat selection by European beaver (*Castor fiber*) colonising a boreal landscape. J Zool 240:317–325

Hartman G, Tornlov S (2006) Influence of watercourse depth and width on dam-building behaviour by Eurasian beaver (*Castor fiber*). J Zool 268:127–131. doi:10.1111/j.1469-7998.2005.00025.x

Hirzel AH, Le Lay G, Helfer V et al (2006) Evaluating the ability of habitat suitability models to predict species presences. Ecol Model 199:142–152. doi:10.1016/j.ecolmodel.2006.05.017

Hood GA, Larson DG (2014) Ecological engineering and aquatic connectivity: a new perspective from beaver-modified wetlands. Freshw Biol 60:198–208. doi:10.1111/fwb.12487

Hyvönen T, Nummi P (2008) Habitat dynamics of beaver *Castor canadensis* at two spatial scales. Wildl Biol 14:302–308. doi:10.2981/0909-6396(2008)14[302:HDOBCC]2.0.CO;2

Iason GR, Sim DA, Brewer MJ, et al (2014). The Scottish beaver trial: woodland monitoring 2009–2013, final report. Scottish Natural Heritage Commissioned Report No. 788

Jiménez-Valverde A, Peterson AT, Soberón J, Overton JM, Aragón P, Lobo JM (2011) Use of niche models in invasive species risk assessments. Biol Invasions 13:2785–2797. doi:10.1007/s10530-011-9963-4

John F, Kostkan V (2009) Compositional analysis and GPS/GIS for study of habitat selection by the European beaver, *Castor fiber* in the middle reaches of the Morava river. Folia Zool 58:76–86

John F, Baker S, Kostkan V (2010) Habitat selection of an expanding beaver (*Castor fiber*) population in central and upper Morava river basin. Eur J Wildl Res 56:663–671. doi:10.1007/s10344-009-0361-5

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957

Jones K, Gilvear D, Willby N, Gaywood M (2003) Felling and foraging: results of the first year of beaver (*Castor fiber*) activity in an enclosed Scottish site. Lutra 46:163–172

Jones K, Gilvear D, Willby N, Gaywood M (2009) Willow (*Salix* spp.) and aspen (*Populus tremula*) regrowth after felling by the Eurasian beaver (*Castor fiber*): implications for riparian woodland conservation in Scotland. Aquat Conserv 19:75–87. doi:10.1002/aqc.981

Kaczensky P (1999) Large carnivore depredation on livestock in Europe. Ursus 11:59–72

Kloskowski J (2011) Human–wildlife conflicts at pond fisheries in eastern Poland: perceptions and management of wildlife damage. Eur J Wildl Res 57:295–304. doi:10.1007/s10344-010-0426-5

Krojerová-Prokešová J, Barančeková M, Hamšíková L, Vorel A (2010) Feeding habits of reintroduced Eurasian beaver: spatial and seasonal variation in the use of food resources. J Zool 281:183–193. doi:10.1111/j.1469-7998.2010.00695.x

Lescureux N, Linnell JDC (2014) Warring brothers: the complex interactions between wolves (*Canis lupus*) and dogs (*Canis familiaris*) in a conservation context. Biol Conserv 171:232–245. doi:10.1016/j.biocon.2014.01.032

Lobo JM, Jiménez-valverde A, Real R (2014) AUC: a misleading measure of the performance of predictive distribution models. Glob Ecol Biogeogr 17:145–151. doi:10.1111/j.1466-8238.2007.00358.x

Macdonald DW, Tattersall FH, Brown ED, Balharry D (1995) Reintroducing the European beaver to Britain nostalgic meddling or restoring biodiversity. Mamm Rev 25:161–200

Macdonald DW, Tattersall FH, Rushton S et al (2000) Reintroducing the beaver (*Castor fiber*) to Scotland: a protocol for identifying and assessing suitable release sites. Anim Conserv 3:125–133. doi:10.1111/j.1469-1795.2000.tb00237.x

Maringer A, Slotta-Bachmayr L (2006) A GIS-based habitat-suitability model as a tool for the management of beavers *Castor fiber*. Acta Theriol (Warsz) 51:373–382. doi:10.1007/BF03195184

Muscarella R, Galante PJ, Soley-Guardia M et al (2014) ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. Methods Ecol Evol 5:1198–1205. doi:10.1111/2041-210X.12261

Niewold F (2007) Graverij van bevers in rivierdijken in de Gelderse Poort. Een onderzoek naar risicofactoren en preventieve maatregelen (**in Dutch**)

Nolet BA, Rosell F (1994) Territoriality and time budgets in beavers during sequential settlement. Can J Zool 72:1227–1237

Nolet BA, Rosell F (1998) Comeback of the beaver *Castor fiber*: an overview of old and new conservation problems. Biol Conserv 83:165–173. doi:10.1016/S0006-3207(97)00066-9

Nolet BA, Hoekstra A, Ottenheim MM (1994) Selective foraging on woody species by beaver (*Castor fiber*) and its impact on riparian willow forest. Biol Conserv 70:117–128

Nummi P, Hahtola A (2008) The beaver as an ecosystem engineer facilitates teal breeding. Ecography (Cop) 31:519–524. doi:10.1111/j.0906-7590.2008.05477.x

Nummi P, Holopainen S (2014) Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. Aquat Conserv 633:623–633. doi:10.1002/aqc.2437

Nummi P, Kattainen S, Ulander P, Hahtola A (2011) Bats benefit from beavers: a facilitative link between aquatic and terrestrial food webs. Biodivers Conserv 20:851–859. doi:10.1007/s10531-010-9986-7

Nyssen J, Pontzeele J, Billi P (2011) Effect of beaver dams on the hydrology of small mountain streams: example from the Chevral in the Ourthe Orientale basin, Ardennes, Belgium. J Hydrol 402:92–102. doi:10.1016/j.jhydrol.2011.03.008

Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. Ecography (Cop) 31:161–175. doi:10.1111/j.2007.0906-7590.05203.x

Phillips SJ, Anderson RP, Schapire RE (2006) Maximum entropy modeling of species geographic distributions. Ecol Model 190:231–259. doi:10.1016/j.ecolmodel.2005.03.026

Pillai A, Heptinstall D (2012) Twenty Years of the Habitats Directive: a case study on species reintroduction, protection and management. Environ Law Rev 15:27–46. doi:10.1350/enlr.2013.15.1.174

Pinto B, Santos MJ, Rosell F (2009) Habitat selection of the Eurasian beaver (*Castor fiber*) near its carrying capacity: an example from Norway. Can J Zool 87:317–325. doi:10.1139/Z09-015

Radosavljevic A, Anderson RP (2014) Making better Maxent models of species distribution: complexity, overfitting and evaluation. J Biogeogr 41:629–643. doi:10.1111/jbi.12227

Rosell F, Bozsér O, Collen P, Parker H (2005) Ecological impact of beavers *Castor fiber* and *Castor canadensis* and their ability to modify ecosystems. Mamm Rev 35:248–276. doi:10.1111/j.1365-2907.2005.00067.x

Schley L (2004) Characteristics of trees and shrubs felled by a Eurasian beaver. Bull Soc Nat luxemb 105:133–136

Sitati NW, Walpole MJ, Leader-Williams N (2005) Factors affecting susceptibility of farms to crop raiding by African elephants: using a predictive model to mitigate conflict. J Appl Ecol 42:1175–1182. doi:10.1111/j.1365-2664.2005.01091.x

South A, Rushton S, Macdonald D (2000) Simulating the proposed reintroduction of the European beaver (*Castor fiber*) to Scotland. Biol Conserv 93:103–116. doi:10.1016/S0006-3207(99)00072-5

Statbel (2010) Structure of the population according to residence: surface and population density. Total population, on January 1 2010. Statistics of Belgium from the federal government

Swinnen KRR, Hughes NK, Leirs H (2015) Beaver (Castor fiber) activity patterns in a predator-free landscape. What is keeping them in the dark? Mamm Biol - Zeitschrift für Säugetierkd 80:477–483. doi:10.1016/j.mambio.2015.07.006

Taylor JD, Singleton RD (2014) The evolution of flow devices used to reduce flooding by beavers: a review. Wildl Soc Bull 38:127–133. doi:10.1002/wsb.363

Treves A, Wallace RB, Naughton-Treves L, Morales A (2006) Co-managing human–wildlife conflicts: a review. Hum Dimens Wildl 11:383–396. doi:10.1080/10871200600984265

Ulevičius A, Kisielytė N, Jasiulionis M (2011) Habitat use and selectivity by beavers (*Castor fiber*) in anthropogenic landscape. Ekologija 57:47–54. doi:10.6001/ekologija.v57i2.1884

Václavík T, Meentemeyer RK (2012) Equilibrium or not? Modelling potential distribution of invasive species in different stages of invasion. Divers Distrib 18:73–83. doi:10.1111/j.1472-4642.2011.00854.x

Verbeylen G (2003) The unofficial return of the European beaver (*Castor fiber*) in Flanders (Belgium). Lutra 46:123–128

Vlaamse Regering (2015) Soortbeschermingsprogramma voor de Europese bever (*Castor fiber*) in Vlaanderen

Warren DL, Seifert SN (2011) Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. Ecol Appl 21:335–342. doi:10.1890/10-1171.1

Willby NJ, Casas Mulet R, Perfect C (2011) The Scottish beaver trial: monitoring and further baseline survey of the aquatic and semi-aquatic macrophytes of the lochs 2009

Wils C, Paelinckx D, Adams Y, et al (2006) Biologische Waarderingskaart van het Vlaamse Gewest. Instituut voor Natuur-en Bosonderzoek (INBO), Brussels

Wright J, Jones C, Flecker A (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101. doi:10.1007/s00442-002-0929-1

Yoccoz NG, Nichols JD, Boulinier T (2001) Monitoring of biological diversity in space and time. Trends Ecol Evol 16:446–453. doi:10.1016/S0169-5347(01)02205-4

Zhang L, Wang N (2003) An initial study on habitat conservation of Asian elephant (*Elephas maximus*), with a focus on human elephant conflict in Simao, China. Biol Conserv 112:453–459. doi:10.1016/S0006-3207(02)00335-X