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Species distribution models as a tool to predict range expansion after reintroduction: a case study on Eurasian beavers (*Castor fiber*)

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## Abstract

Species Distribution Models (SDMs) may provide important information for the follow-up phase of reintroduction operations by identifying the main areas most likely to be colonized by the reintroduced species. We used SDMs to identify the potential distribution of Eurasian beavers (*Castor fiber*) reintroduced to Serbia and Bosnia and Herzegovina in 2004-2006 after being historically driven to extinction by overhunting. Models were also used to carry out a gap analysis to assess the degree of protection granted by the national reserve networks to the potentially expanding population. Distances from hydrographic network, broadleaved forest, main watercourses and farmland were the main factors influencing model performance. We estimated that suitable habitat covers 14.0 % (31,000 km<sup>2</sup>) of the whole study area. In Serbia, in 2004-2013 beavers expanded their range at a mean colonization speed of  $70.9 \pm 12.8$  km/year (mean  $\pm$  SD). Only 2.89% of and 9.72% of beaver's suitable habitat lie within the national network of protected areas of Bosnia and Serbia respectively. We detected new potential areas where beavers will likely settle in the near future, advising on where further

monitoring should be focused. We also identified low suitability areas to be targeted with appropriate management to improve their conditions as well as important regions falling outside reserve boundaries where protection should be granted.

**Keywords:** Bosnia and Herzegovina; Conservation gap analyses; Habitat suitability; Riparian habitats; Serbia.

## 1. Introduction

Reintroduction— i.e. the intentional translocation of species into parts of their historically known range from which they have been extirpated (IUCN/SSC, 2012) – is one of the key strategies adopted to restore biodiversity and ecosystem functioning. Forecasting the expansion of a reintroduced species over a given region as part of reintroduction’s follow-up phase may be essential to anticipate events that might otherwise jeopardise the operation’s success in order to secure appropriate protection in the newly colonised areas, prevent conflicts with humans, optimise monitoring strategies and apply adaptive management of habitat quality (e.g. Breitenmoser et al., 2001; McCarthy et al., 2012; Armstrong & Reynolds, 2012).

Habitat suitability mapping is frequently used to inform habitat restoration or preservation actions (Gibson et al., 2004) or to identify suitable sites for species reintroduction (e.g. Olsson & Rogers, 2009; Ardestani et al., 2015). This approach has become an important component of conservation planning in recent years, and a wide variety of modelling techniques have been developed for this purpose (Guisan & Thuiller, 2005; Elith et al., 2006; Elith & Leathwick, 2009). Although Species Distribution Models (hereafter SDMs) appear to be a promising tool to guide the planning of reintroduction operations by conservation biologists and landscape managers, so far their applications to this field have been scarce (see e.g. Wilson et al., 2011; Adhikari et al., 2012). Such models may predict the probability of species presence by relating current occurrences and environmental features at sample locations (Guisan & Zimmermann, 2000; Phillips et al., 2006). In this way the areas that are more likely to be re-colonised as well as the most probable routes followed in the process can be

forecast, drawing valuable inferences on the establishment, expansion and persistence of a reintroduced species (Armstrong & Seddon, 2008).

A clear understanding of species-habitat relationships makes it possible to identify highly suitable release sites that offer the maximum chance of post-release survival or guide habitat restoration prior to reintroduction (Seddon et al., 2007).

Despite the outstanding potential of SDMs in predicting the expansion of a newly introduced species to a given region (Armstrong & Reynolds, 2012), their use to achieve this goal has been largely neglected. In our study we apply SDMs to assess the post-release expansion of Eurasian beavers (*Castor fiber*) in Serbia and Bosnia and Herzegovina and evaluate the potential role of nature reserves to assist this process. The species was once common across Eurasia from the British Isles to eastern Siberia, inhabiting freshwater habitats surrounded by forest but also reaching into the tundra and steppe zones (Nolet & Rosell, 1998; Macdonald & Barrett, 1993; Macdonald et al., 1995; Halley & Rosell, 2002). Prized for its fur, meat and castoreum (a urine-based fluid secreted from castor sacs for scent marking valued by humans for medic or cosmetic applications), beavers were wiped out by overhunting from most of their range by the middle 19th century (Djoshkin & Safonov, 1972). By the beginning of the 20th century, only 1200 individuals had persisted in eight isolated populations across the entire species' range (Nolet & Rosell, 1998). The remnant populations received legal protection, and since 1922 reintroductions started in many European regions to pursue species conservation and ecosystem restoration (Kollar & Seiter, 1990; Nolet & Rosell, 1994; Halley & Rosell, 2002). To date, the return of *C. fiber* has not yet taken place only in Portugal, Italy, southern Balkans (Greece, Albania, Bulgaria, Macedonia and Montenegro) and Ireland (Halley & Rosell, 2002; Halley et al., 2012), while two wild populations now occur in Scotland on a trial basis (Stringer & Gaywood, 2016). Currently, the species is strictly protected in the European Union under the Bern Convention (Appendix III) and the EU Habitats and Species Directive (Annex V for the Swedish and Finnish populations, Annex II and IV for all others).

The Serbian population of beavers was driven to extinction by overhunting by the second half of the 19th century, apart from an unconfirmed report of a beaver shot near Belgrade at the beginning of the last century (Ćirović et al., 2003,2007). By then, the species had also disappeared from the whole course of the Danube and

its tributaries. In 1999, following the shooting of a beaver in Northern Serbia (Vojvodina, Bačka region) that had dispersed from the re-established population of Hungary, a reintroduction operation was started in Serbia and Bosnia and Herzegovina (Ćirović et al., 2001,2003). In 2004 and 2005, 75 subjects imported from Bavaria were reintroduced to the Obedska Bara and Zasavica Special Reserves in Serbia, and 40 were released in Semešnica and Sokočnica rivers in Bosnia and Herzegovina in 2005 and 2006 (Appendix S1).

Although many studies have assessed beaver habitat requirements (Zurowsky & Kasperczyk, 1990; Parker et al., 2001; Fustec et al., 2001; Vorel et al., 2008; Halley et al., 2012) only few applications of habitat suitability models have been carried out, e.g.in the Czech Republic (John et al., 2010) and Austria (Maringer & Slotta-Bachmayr, 2006). In our study, we quantify the potential distribution of *C. fiber* for Serbia and Bosnia and Herzegovina to predict the species' spatial pattern of expansion. We hypothesize that 1) given the overwhelming importance of riparian habitat and the tendency of beavers to feed on crops (Campbell-Palmer et al. 2016), hydrographical network, riparian broadleaved forest and farmland will be the main environmental variables influencing potential distribution; and that 2) since most reserves in the study region do not comprise rivers, the network of protected areas will offer little protection to the aforementioned distribution.

## 2. Materials and Methods

### 2.1. Study area

The study area included the whole territories of Serbia and Bosnia and Herzegovina, covering approximately 139570 km<sup>2</sup> between latitudes 41°N-47°N and longitudes 15°E-23°E. Elevation ranges from 0 up to 2500 m a.s.l. The area is largely mountainous and forested (c. 50% of Bosnia and 25% of Serbia). Arable land covers 53.2% of Serbia and 28.7% of Bosnia and Herzegovina (Corine land cover 2006, <https://www.eea.europa.eu>). Agricultural production is mostly prominent in the fertile Pannonian Plain situated in the northern part of Serbia (Vojvodina) and in the region of Serbia between the Sava, Drina and Great Morava rivers, while in Bosnia farmland is found in the valleys of Sava, Una, Sana, Vrbas, Bosna and Drina rivers.

## 2.2. Presence records of the Eurasian beaver

We used 71 presence records of Eurasian beavers from authors' personal databases obtained from the post-reintroduction monitoring in Serbia and Bosnia and Herzegovina (Grubešić et al., 2015) (Fig. 1). Records cover years 2004-2014, matching the year of production (2006) of the land cover map used for our study (Russo et al., 2014, 2015).

Each record represented the centroids of a beaver's territory, corresponding to a beaver's shelter (burrow or lodge) or, if this was not found, to the central part of the winter feeding territory. We checked for spatial autocorrelation in species occurrences by using Clark & Evans(1954)'s aggregation index – for further details, see also Ducci et al. (2015) and Di Febbraro et al. (2015).

We implemented a sampling procedure to obtain a representative set of the environmental conditions occurring throughout the area of each territory. Specifically, we defined the boundaries of each territory by intersecting two buffer areas:

- i) a first 1.7km radius circular buffer was drawn around each occurrence record, whose intersections with the watercourse's main axis were assumed to represent the territory's outer limits along the watercourse. The 1.7km value corresponds to the maximum length known for a beaver's linear territory (Vorel et al., 2008);
- ii) a second 200-m buffer from each river bank was applied to encompass the territory portions alongside the river stretch, expressing the maximum territory width observed in the study area. This is approximately the longest distance covered by beavers from riverbanks to forage according to published observation and our own records (Allen 1983; D. Ćirović, unpublished data). Subsequently, a point was taken randomly from each of the areas comprised within the above buffers, repeating this sampling procedure 10 times and obtaining 10 independent sets of 45 "occurrence" points, one for each territory. Each of the 10 replicated sets was used to train a separate SDM.

To fit SDMs with the global scale (Gallien et al., 2012 – see below), we used GBIF records (Appendix S2).

## 2.3. Environmental variables

To generate SDMs we started from a set of 13 environmental predictors rasterized at a resolution of 100 m, including five topographical and seven habitat classification variables, in combination with the hydrographical network. The topographic predictors included a Digital Elevation Model (DEM) derived by Jarvis et al. (2008), from which altitude and slope were taken, and the following additional topographical indices (Wilson et al., 2007): Terrain Ruggedness Index (TRI), Topographic Position Index (TPI) and roughness index. Habitat predictors were calculated as Euclidean distances from the 2006 Corine Land Cover classes (European Environmental Agency; <http://www.eea.europa.eu/data-and-maps/data/corine-land-cover-2006-raster>) and from the hydrographic network of the Digital Chart of the World (DCW; <http://www.diva-gis.org/gdata>). The 13 predictors were checked for pairwise correlation and reduced to 11 considering a variance inflation factor less or equal to three (Zuur et al., 2010).

In order to choose the most appropriate set of environmental predictors, we developed a variable selection procedure taking into account model performance and overfitting (Appendix S3). The variable selection procedure identified the following six predictors (Table 1) as those producing the best models: Elevation and Euclidean distance from hydrographic network, main watercourses, farmlands, inland marshes and broadleaved forests.

#### 2.4. Modelling procedure

A growing amount of literature highlights that environmental truncation in niche estimation for areas encompassing only a small portion of a species' global range produces severely biased predictions (Barbet-Massin et al., 2010; Raes, 2012; Guisan et al., 2014). As *C. fiber* is distributed across the Palearctic (IUCN, 2012) and our study area represents a small portion of the entire range, SDMs were produced using a hierarchical structure from a global to regional scale (Pearson et al., 2004; Lomba et al., 2010; Gallien et al., 2012, Di Febbraro et al., 2015). Following this approach, models were first implemented to estimate the species' niche at their global range scale using bioclimatic variables (Global SDMs; further details are provided in Appendix S2), then refined at a regional scale using land cover, hydrographical network and topographical variables as environmental predictors (Regional SDMs; Pearson et al., 2004; Lomba et al., 2010; Gallien et al.,

2012, Di Febbraro et al., 2015). Regional SDMs were developed using an ensemble forecasting approach, as implemented in the package "biomod2" in the R software (R Development Core Team, 2009) (Thuiller et al., 2009). Biomod2 is a modelling platform that makes it possible to train SDMs using different modelling techniques, as well as to evaluate them and perform different averaged outputs of the single-model predictions (see Thuiller et al., 2009). Using different statistical methods to model species distribution is highly recommended as prediction discrepancies between different techniques can be very large (Araujo et al., 2005; Thuiller et al., 2009). We considered the following seven modelling techniques (Thuiller et al., 2009; Jiguet et al., 2010; Ducci et al., 2015): (1) generalized linear models (GLM); (2) generalized additive models (GAM); (3) generalized boosted models (GBM); (4) random forests (RF); (5) multivariate adaptive regression spline (MARS), (6) maximum entropy models (MAXENT) and (7) BIOCLIM (Surface Range Envelope, SRE) – for further details, see Thuiller et al. (2009).

Following Pio et al. (2014), the modelling settings were tuned as follows. GLMs and GAMs were calibrated using a binomial distribution and a logistic link function. GBMs were calibrated with a maximum number of trees set to 5000, threefold cross-validation procedures to select the optimal numbers of trees to be kept and a value of seven as maximum depth of variable interactions. Random forest models were fitted by growing 750 trees with half the numbers of available predictors sampled for splitting at each node. MARS models were fitted with a maximum interaction degree equal to 2, MAXENT models were fitted with the default settings apart of a maximum value of 1000 iterations and default parameters were used to fit the SRE model.

Each occurrence dataset was randomly split into a 70 % sample, used for the calibration of the model, and the remaining 30 %, used to evaluate model performance. A set of 10,000 background points were randomly placed in the study area to characterize its environment and represent pseudo-absences. According to Gallien et al. (2012), these background points were not considered 'true' absences, i.e. we assumed that some absences probably reflect environmental conditions where the species cannot survive, while others reflect locations where the species has not been surveyed due to imperfect detection. These pseudo-absences were weighted by the committee averaging projections calculated with the Global SDMs (Appendix S2): where the Global SDMs showed a high level of agreement with an absence (i.e. a low habitat suitability) we attributed a high weight to

that absence (i.e. a high probability of being a ‘true’ absence), and vice versa. The weight was calculated by an inverse logistic transformation (equation 1) to obtain a stronger discrimination between the predictions of absences and presences (Gallien et al., 2012):

$$\text{Weight}(x) = \frac{1}{1 + \left(\frac{\text{projGlob}(x)}{\text{projGlob}(x)-1}\right)^2} \quad (1)$$

where  $\text{Weight}(x)$  is the weight attributed to the pseudo-absence  $x$ , which depends on  $\text{projGlob}(x)$ , the prediction of the Global SDMs at the location of  $x$  [if  $\text{projGlob}(x) = 1$  then  $\text{Weight}(x) = 0$ ].

The models’ predictive performances were assessed by measuring the area under the receiver operating characteristic curve (AUC) (Hanley & McNeil, 1982) and the true skill statistic (TSS) (Allouche et al., 2006).

These validation methods have been widely used (e.g. Russo et al., 2014, 2015; Feuda et al., 2015; Bosso et al., 2016 a, b) and offer excellent performances. The data splitting procedure was repeated 10 times and the evaluation values averaged. For each of the 10 replicates of the species’ dataset, we ran a total of 70 Regional SDMs (seven algorithms x 10 splitting replicates for model evaluation). Model averaging (ensemble model) was performed by weighting the individual model projections by their AUC scores (only models with  $\text{AUC} \geq 0.8$ ) and averaging the result—a method shown to be particularly robust (Marmion et al., 2009). The relative importance of variables was also calculated from the ensemble model using the specifically devoted functionality available in the *biomod2* package (Jiguet et al., 2010). The final projected distribution of the species was obtained by averaging the projections from our 10 replicated ensemble models. This final map was also transformed into presence-absence values using a threshold maximizing sensitivity (the percentage of correctly predicted presence) and specificity (the percentage of correctly predicted absence) (Fielding & Bell, 1997). Such threshold has been widely used (e.g. Algar et al., 2009; Dubuis et al., 2011; Di Febbraro et al., 2015) and constitutes one of the most accurate approaches (Liu et al., 2005).

## 2.5. Assessment of potentially colonized suitable habitat

In order to discriminate predicted suitable areas already potentially colonized by beavers from those potentially colonizable in the future, we estimated the approximate distance covered by the beaver population since the release until the year of the most recent available record. For this analysis, we used only 39 records of beavers reintroduced to Serbia, because for Bosnia and Herzegovina we had gaps in the dataset for some years (2008 and from 2011 to 2013), and we also discarded some locations of subjects originated from Croatia and Hungary. First, we pooled the species' presence records according to their recording date in two-years groups from 2004 to 2013, obtaining 8 groups of points. Subsequently, we calculated the maximum distance between all the points within each group ("spDists" function in the sp package; Pebesma & Bivand, 2005). This represents the maximum distance covered by beavers in one year. Starting from the set of maximum distances calculated in this way, we computed the minimum, mean and maximum distance values, then generated three buffers around all occurrences points used for analysis with the "gBuffer" function of rgeos package (Bivand & Rundel, 2013). Suitable pixels falling inside the buffers refer to areas already potentially colonized by beavers up to 2014 (i.e. the year following that of the most recent available record). On the contrary, suitable areas placed beyond the maximum dispersal distance estimated up to 2014 (i.e. outside the buffers) represent areas that might be colonized by the species in the future.

## 2.6. Conservation gap analyses

To assess the degree of protection granted to Eurasian beavers by the reserve network of Serbia and Bosnia and Herzegovina, we carried out two conservation gap analyses, one based on the actual occurrence maps, the other based on the binarized potential distribution map (e.g. Bosso et al., 2013; Bosso et al., 2016c). We overlaid such maps with the shape files containing the boundaries of the nature reserves of Serbia and Bosnia and Herzegovina. The shape files of the protected areas for these two countries were downloaded from <http://www.protectedplanet.net/> (UCN and UNEP-WCMC, 2016). We included national parks, Ramsar Network Areas (<http://www.ramsar.org/activity/ramsar-culture-network>) and Reserves (Natural, Managed Nature, Strict Nature and Special Reserves).

### 3. Results

#### 3.1. Model performances and habitat suitability

Both Global and Regional SDMs showed good or excellent levels of predictive performance as indicated by the AUC and TSS values. AUC and TSS for Global SDMs had a mean value and a standard deviation respectively of  $0.813 \pm 0.019$  and  $0.537 \pm 0.042$ , whereas evaluation scores for Regional SDMs were equal to  $0.968 \pm 0.006$  and  $0.824 \pm 0.021$ . According to our hypothesis, the environmental predictors that were most important to explain the beaver's potential distribution were distances from hydrographic network, broadleaved forests and farmland. The species was also predicted to occur most likely at lower altitudes (Fig. 2), but might reach 1000 m a.s.l. in the suitable areas of Southern and Eastern Serbia (Šar mountain in the south and Stara planina mountain in the east) and Western Bosnia (Dinaric Alps) (Fig. 3, Appendix S1). In general, habitat suitability decreased for increasing distances from hydrographic network, broadleaved forests, agricultural lands, main watercourses and inland marshes. For main watercourses, the variable's response curve also showed a second peak at greater distances, likely corresponding to the places where secondary tributaries occurred (Fig. 2). Regional model predictions showed that the most suitable areas were concentrated in Northern Serbia and Bosnia and Herzegovina along the main rivers (i.e. Danube, Sava, Tisa and Drina rivers) and their tributaries, in Central Serbia and Bosnia and Herzegovina along the Great Morava, Bosna, Vrbas, Una and Sana Rivers and in Southern Serbia and Bosnia and Herzegovina along secondary river courses such as Neretva and Beli Drim Rivers, as well as many Great Morava's tributaries (Fig. 3, Appendix S1). The percentage of suitable habitat for the beaver accounts for ca. 14% (~31,000 km<sup>2</sup>) of the whole study area.

When taken separately, outputs of the algorithms employed to implement the ensemble model all predicted a high amount of suitable habitat in Southern, South-eastern and Central regions of Serbia (Sar mountain and Beli Drim, Danube, Sava and Morava Rivers) and in Central-western regions of Bosnia (Sana and Sokočnica Rivers). Unsuitable areas were mostly detected for Northern Serbia and North-western Bosnia (Appendices S1, S4). The most restrictive predictions were provided by Random Forest (RF) and Generalised Boosting Models

(GBM) whereas Generalised Linear Model (GLM) and Generalised Additive Model (GAM) detected suitable habitat mostly along the main rivers as well as their tributaries.

### *3.2. Assessment of potentially colonized suitable habitat*

From 2004 to 2013 the dispersal distances travelled by the species ranged between 56.61-88.28 km/year with a mean colonization speed of  $70.9 \pm 12.8$  km/year (mean  $\pm$  SD). According to minimum, mean and maximum dispersal distances potentially covered by beavers since their release up to 2014 (ca. 35% of the all suitable area; Figure 4) individuals from Serbia might have reached the suitable areas of Central Bosnia and Herzegovina since the last occurrence of 2013 had they dispersed at the maximum estimated speed. Within this portion of territory, they would have been more likely to colonize the northern part of Serbia and Bosnia and Herzegovina where more suitable areas occur, especially along the Danube, Tisa and Sava Rivers, exploiting the structural connectivity offered by the hydrographic network. According to the maximum distance buffer, beaver's populations could have reached large portions of Central-Eastern Serbia, especially along the Great Morava river and its tributaries. By 2014, therefore, the species might have reached the borders of the country in the north-western part of the study area, joining individuals from Croatia. Large parts of South-Eastern Serbia beyond the maximum dispersal distance estimated up to 2014 are also suitable for beavers, so they might be colonized in the future.

### *3.3. Conservation gap analyses*

As hypothesised, the country's reserve network offers little protection to the species (Table 2). Specifically, no presence records for Bosnia and 39.06% of those for Serbia lie within the boundaries of the national network of protected areas, while only 2.89% of Bosnian and 9.72% of Serbian suitable habitat fall within this network. In

particular, beavers occur in the Serbian Special Natural Reserves of Zasavica and Obedska bara, where they were reintroduced, and in the Fruška Gora National Park in the northern part of the country near Croatia (Fig. 5a, Appendix S1). In Serbia, small portions of suitable habitat lie in the Natural Reserves and National Park previously mentioned in the north as well as along river valleys in the Šar planina National Park and Stara Planina Nature Park, respectively in south and eastern Serbia (Fig. 5b, Appendix S1). A very small portion of suitable habitat in Bosnia and Herzegovina falls within three Ramsar sites (a list of wetlands of international importance) and in the Kozara National Park in the country's northern part between Sava and Vrbas Rivers.

#### 4. Discussion

We found that a wide area of Serbia and Bosnia and Herzegovina predicted as suitable for beavers might be colonized in the near future, especially in Central and Southern Serbia. Our analysis highlighted that beavers have remarkable colonization skills, demonstrated by a very high dispersal distance travelled soon after reintroduction, which allows them to reach quickly optimal habitat found far from the release sites. From a conservation point of view, expanding beavers could potentially be at risk in both Serbia and Bosnia and Herzegovina since the national network of protected areas does not grant sufficient protection to both currently occupied areas and those of potential future colonization.

We confirmed the hypothesis that beaver habitat suitability is mostly influenced by the presence of rivers, broadleaved forests and farmlands, as shown by previous studies (Fustec et al., 2001; Maringer & Slotta-Bachmayr, 2006; Vorel et al., 2008; John et al., 2010). For instance, South et al., (2000) developed a spatially explicit model to explore the possibility of reintroducing beavers to Scotland using an individual-based population dynamics module integrated with GIS data on the spatial distribution of habitat. As in our case too, sites with sufficient deciduous woodlands adjacent to rivers were classified as suitable for the beaver. Besides, field observations carried out in the Netherlands showed that territories occupied by a single beaver family include at least ca. 2 km of wooded banks (Nolet & Rosell, 1994). Although some studies concluded that vegetation type contributes little to beaver habitat models and highlighted the importance of geomorphologic river variables like water depth, slope of river banks and interbank distance (Beier & Barrett, 1987; Hartman,

1996; Suzuki & McComb, 1998), John et al. (2010) found that beavers actively sought out areas dominated by willows (*Salix* spp.) during their expansion phase along the Morava River basin (Czech Republic). This result is further confirmed by previous observations (Zurowski & Kasperczyk, 1990) showing that a recently reintroduced beaver population may tolerate environments with extreme water fluctuations to settle close to willow patches. We therefore remark that broadleaved forest habitat should be regarded as an important predictive variable for beaver settlement in both optimal and suboptimal/marginal habitat during expansion phases before a population reaches its carrying capacity.

The importance of farmland is associated with the species' ecological flexibility (Nolet & Rosell, 1998): crops constitute important food sources when close (within c. 20m) to river banks where beavers have settled (Schwab & Schmidbauer, 2003), especially where natural food is scarce (Dewas et al., 2012).

The mean estimated dispersal distance of ca. 70 km travelled by beavers in a year is in agreement with the results of previous studies. For instance, Fustec et al. (2001) estimated a maximum distance travelled by colonizing beavers for the Loire Valley between 0-80 km/year. On the other hand, the annual colonization speed estimated by John et al. (2010) in the Morava River basin from 1995 to 2007 was lower (0-33 km). Our greater values refer to the first ten years following reintroduction, when range expansion typically proceeds at a faster pace (Halley & Rosell, 2002; Hartman, 1995). The long dispersal distances we obtained may also be due to the fact that shortly after reintroduction beavers follow a spatially discontinuous dispersal pattern often colonising optimal sites farther away from closer, less suitable sites (Nolet & Rosell, 1994; John et al., 2009, 2010). This kind of expansion pattern appears particularly relevant for management, as beavers released in suboptimal habitats are likely to cover long distances to settle farther away where better environmental conditions occur (Halley & Rosell, 2002).

The need for appropriate management to favour beavers' expansion in Serbia and Bosnia and Herzegovina is also remarked by further consideration. Beavers are ecosystem engineers in aquatic habitats because they modify riverine and wetland habitats favouring many other species by felling trees (Fustec et al., 2001; John et al., 2010) and building dams that create still water conditions (Rosell et al., 2005; Stringer & Gaywood, 2016; Law et al., 2016). Their impact on forests and cultivations, however, as well as their tendency to settle near

human-dominated areas may also generate conflicts with humans (Schwab & Schmidbauer, 2003; Dewas et al., 2012) and increase beaver mortality. Both in Serbia and Croatia beavers are often killed by collision with motor vehicles and entanglement in fishing nets. Most kills occur in spring, when sub-adults are more active in food search and explore new sites, and autumn, when increased agricultural practices expose beavers to be killed by vehicles or farmers (Grubešić et al., 2015). Conflicts might be mitigated by improving the current network of protected areas, which unfortunately is largely insufficient in agreement with our second hypothesis. Appropriate management, such as restoring riparian habitats where needed to reduce crop damage and erecting physical barriers to protect crops would also help reduce conflicts and human-induced mortality (Dewas et al., 2012).

Using occurrence records of a beaver population during colonization (not in equilibrium with the environment), might violate one of the main assumptions of SDMs (Guisan & Zimmermann, 2000), but we overcame this shortcoming by using a hierarchical approach in which weights of pseudo-absences are adjusted according to a large-scale climatic model based also on records of populations that have reached the equilibrium. Moreover, although ca. 30-50 years are needed for complete colonization to occur (Hartman, 1995; Halley & Rosell, 2002), the first areas to be colonized are the most suitable ones, regardless of their distance from the release site (Nolet & Rosell, 1994; John et al., 2009; John et al., 2010). Overall, we are confident that our SDMs were reliable.

We inevitably considered the environment as isotropic with respect to species expansion (i.e. the species has the same probability to expand in all the directions). Recent observations suggest that the area predicted to have been occupied by 2014 has in fact only partly been colonized (D. Ćirović, *pers. obs.*), most likely due to the obviously anisotropic nature of the landscape: for example, gaps between rivers may have slowed down colonization. More accurate forecasts would require the application of a specific connectivity model. Nevertheless, quantifying dispersal distances increased the management value of the SDM, helping to identify which areas might have been already occupied and thus target them with urgent monitoring and protection. This might be especially important to generate an action plan setting priorities for the establishment of conservation actions.

Based on our findings, we urge that the current reserve network is expanded further to assist the colonisation process, reduce mortality and mitigate potential conflicts with people. We therefore remark that accession of the two states to the EU would represent a unique chance to assist the further establishment of beavers through the designation of Natura 2000 sites.

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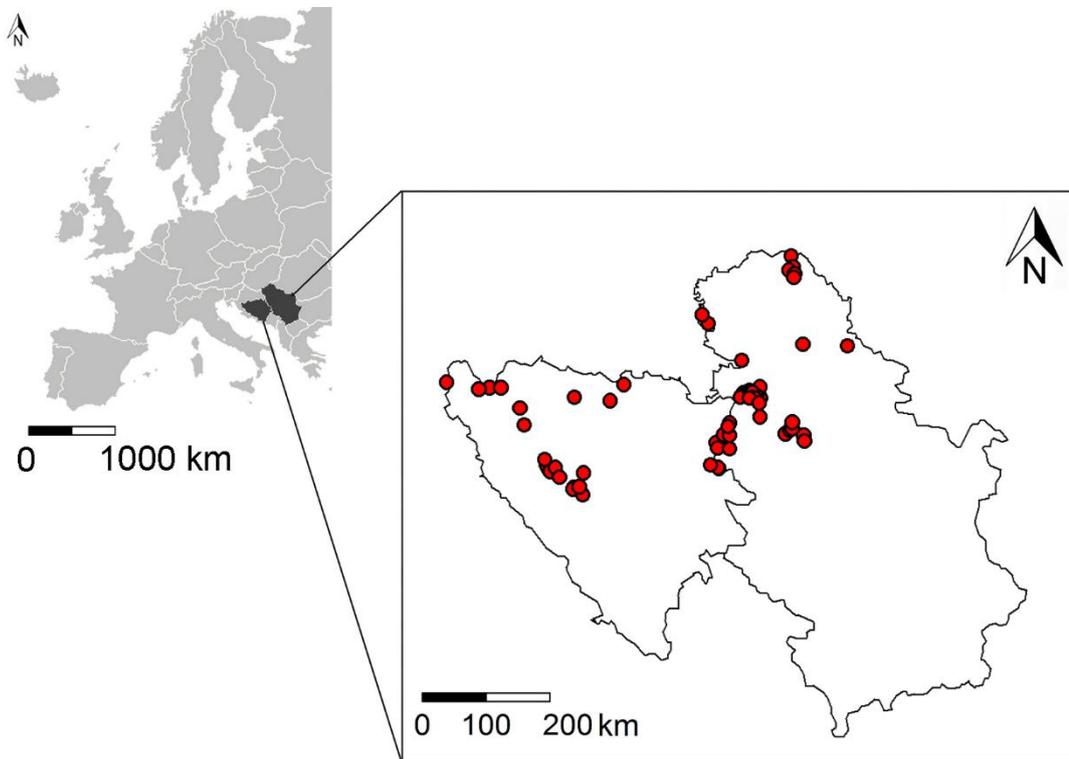
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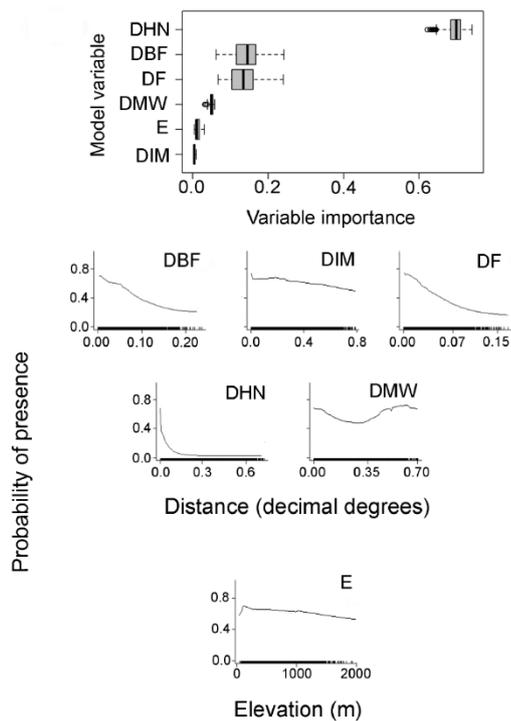
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**Figure Captions**

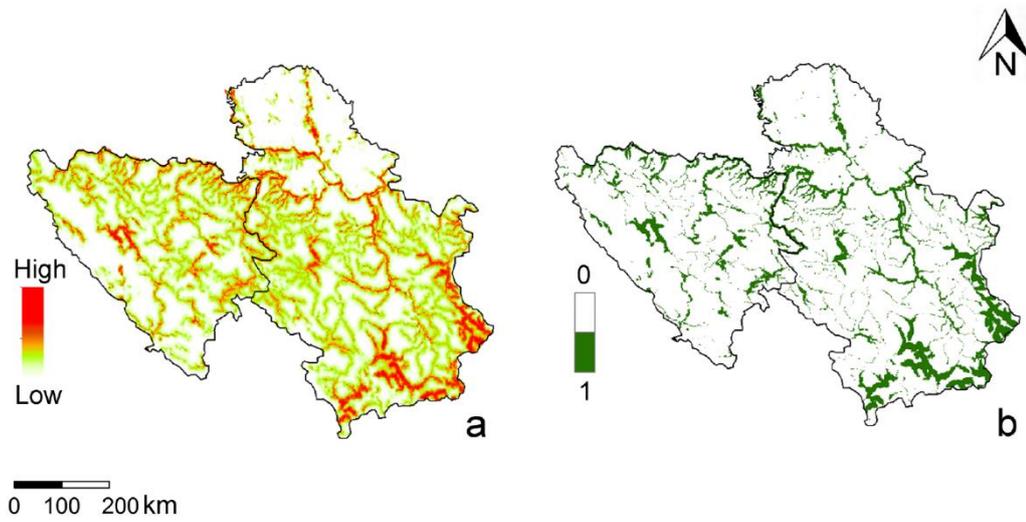
**Fig.1.** Geographic regions (Serbia and Bosnia and Herzegovina) and *Castor fiber* presence records considered for modelling.



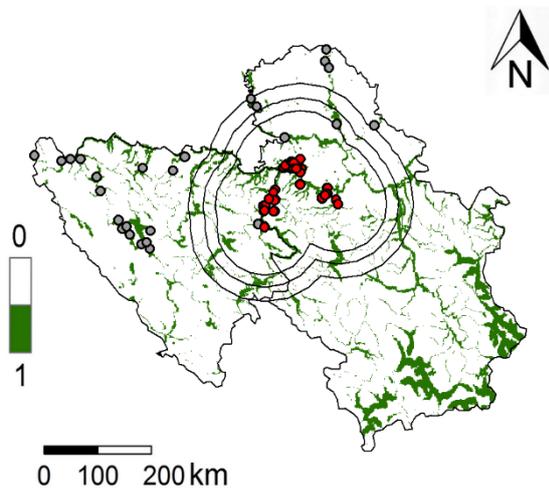
**Fig. 2.** Box plot and response curves for the six variables used to model *Castor fiber* potential distribution in Serbia and Bosnia and Herzegovina with the “biomod2” computer platform. The Box plot (top) expresses variable importance (variables are listed in decreasing order of importance from top to bottom). Response curves (bottom) correlate probability of occurrence (y axis) with values of the explanatory variables (x axis). Each curve represents one variable (DBF = distance from broadleaved forest; DIM = distance from inland marshes; DF = distance from farmlands; DHN, = distance from hydrographic network; DMW = distance from main watercourses; E = elevation). Distances are expressed in decimal degrees, elevation in m a.s.l.



**Fig. 3.** SDM output for *Castor fiber* in Serbia and Bosnia and Herzegovina (a) and presence/absence binary map (b) obtained using the TSS metrics as a threshold.



**Fig. 4.** Potential dispersal distances of beavers projected to year 2014 representing the minimum, mean and maximum colonization speeds. The buffers are computed considering only Serbian occurrences (red filled circles) and excluding those derived from Bosnia, Hungary and Croatia (grey filled circles).



**Fig. 5.** Percentage of *Castor fiber* presence records (red filled circles) (a) and suitable habitat (green areas) (b) and their overlay with networks of protected areas (simple hatch) for Serbia and Bosnia and Herzegovina.

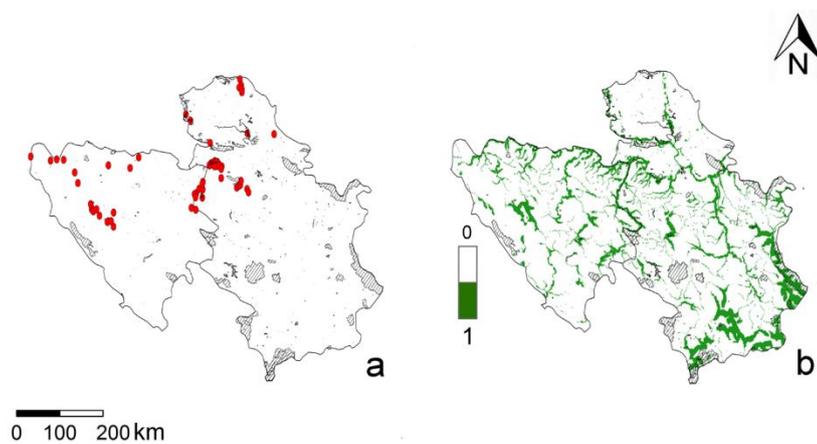


Table 1. List of ecogeographical variables used for the Regional SDMs, their type, index (name used to indicate the variable in the analysis), spatial resolution, and CLC (Corine Land Cover) code. All variables are expressed in m.

Type	Ecogeographical variable	Index	Spatial resolution (km)	CLC code
Topographical	Altitude	Elevation	1	-
Habitat	Distance from hydrographic network	dist_Rivers	1	-
Habitat	Distance from main water courses	dist_Water_courses	1	40
Habitat	Distance from farmlands	dist_Land_principally_agriculture	1	21
Habitat	Distance from Broad-leaved forest	dist_Broad.leaved_forests	1	23
Habitat	Distance from inland marshes	dist_Inland_marshes	1	35

**Table 2.** Degree of protection granted to *Castor fiber* by the network of protected areas of Serbia and Bosnia-Herzegovina based on the current occurrence records and on the binarized map obtained from SDMs. Reserve = Natural, Managed Nature, Strict Nature and Special reserves.

Occurrence records	% records within site			
	National parks	Ramsar Networks	Reserves	All
Geographic area				
Serbia	6.68	0.00	32.38	39.06
Bosnia and Herzegovina	0.00	0.00	0.00	0.00
Species Distribution Models	% suitable surface area within site			
Serbia	5.88	0.00	3.84	9.72
Bosnia and Herzegovina	0.91	1.89	0.09	2.89