Animal Conservation

Animal Conservation. Print ISSN 1367-9430

Environmental suitability and potential range expansion of the Eurasian beaver in Italy

Mattia Falaschi[1], Gentile Francesco Ficetola[1,2], Andrea Viviano[3,4], Giuseppe Mazza[5,6] & Emiliano Mori[3,6]

1 Department of Environmental Science and Policy, Università degli Studi di Milano, Milan, Italy
2 Univ. Grenoble Alpes, Univ. Savoie Mont Blanc, CNRS, LECA, Laboratoire d'Écologie Alpine, Grenoble, France
3 National Research Council, Istituto di Ricerca sugli Ecosistemi Terrestri, Florence, Italy
4 Department of Agricultural, Food, Environmental and Forestry Sciences and Technologies, University of Florence, Florence, Italy
5 CREA Research Centre for Plant Protection and Certification (CREA – DC), Cascine del Riccio (Firenze), Italy
6 National Biodiversity Future Center, Palermo, Italy

Keywords
Castor fiber; climate suitability; connectivity analysis; reintroductions; species distribution model; rewilding; ecosystem engineer; human–wildlife conflict.

Correspondence
Mattia Falaschi, Department of Environmental Science and Policy, Università degli Studi di Milano, Via Celoria 10, Milan 20133, Italy.
Email: matt_fala@hotmail.it

Editor: Karl Evans
Associate Editor: María del Mar Delgado

Received 22 February 2023; accepted 01 September 2023

doi:10.1111/acv.12910

Abstract

Reintroduction and rewilding initiatives are key strategies to reverse human impacts on ecosystems and re-establish natural processes. However, rewilding may involve complex management scenarios, because many expanding species can have economic impacts and cause human–wildlife conflicts. Conflicts can be particularly challenging when carnivores, large herbivores and ecosystem engineers are involved. The Eurasian beaver (*Castor fiber*) is a key ecosystem engineer that was once present in a large part of the Palearctic, but in Medieval times underwent a severe decline due to the joint effects of habitat loss and hunting. Subsequent legal protection and reintroductions triggered the recovery of the species through most of its original range. Eurasian beavers recently started the recolonization of Italy, because of the joint effects of natural dispersal (from Austria to northern Italy) and illegal reintroductions (central Italy). The lack of data on the most likely colonization routes hampers appropriate management of this species. Here, we identified the areas where beaver populations are most likely to arrive in the near future within Europe, with a specific focus on Italy. First, we developed spatially cross-validated species distribution models to identify the areas with the highest suitability for the Eurasian beaver in Europe. Second, we used connectivity modelling to assess the possible expansion routes of this species in Italy. Large areas of Europe are suitable for the beaver and may soon be colonized. The connectivity model showed a high potential for expansion from central Italy to surrounding areas, while the high isolation of northern Italy populations suggests a slower expansion. Our results can help environmental managers to understand where to focus both the future monitoring of beaver populations and actions aimed at preventing and mitigating possible human–wildlife conflicts that could arise from the expansion of an environmental engineer such as the beaver.

Introduction

Global land use and climatic change, together with overexploitation and human-mediated animal translocations, have deeply altered worldwide biogeographical patterns (Higgins, 2007; Young, 2014). Reintroduction and rewilding initiatives are seen as key strategies to reverse human impacts on wildlife and re-establish natural processes, but they may also pose major challenges (Perino *et al.*, 2019). For instance, reintroduced species may conflict with human activities and pose zoonosis risks (Tattoni, Grilli, & Ciolli, 2017; Moseby, Lollback, & Lynch, 2018; Auster, Barr, & Brazier, 2020, 2021; Thulin & Röcklinsberg, 2020). The situation is particularly complex in European landscapes, where the abandonment of agricultural activities in hilly and mountainous areas has led to a substantial expansion of natural vegetation, such as forests, during the last 70 years (Queiroz *et al.*, 2014; Marta *et al.*, 2021). Such land-cover changes have interplayed with ongoing conservation efforts (e.g. species protection, re-introductions), leading to the range expansion of many medium and large-size European mammals (Deinet *et al.*, 2013; Chapron *et al.*, 2014; Cimatti *et al.*, 2021). The expansion of mammals certainly has major impacts on ecosystems, including the re-establishment of interspecific interactions that support ecosystem functioning (Dalbeck, Lüscher, & Ohlhoff, 2007; Chapron *et al.*, 2014; Ripple *et al.*, 2014; Perino *et al.*, 2019). However, rewilding also determines complex management scenarios because many expanding mammals can generate economic impacts and conflicts with human society. These conflicts can be particularly challenging when carnivores, large herbivores and ecosystem engineers are involved (Nawaz, Swenson, & Zakaria, 2008; Ficetola *et al.*, 2014; Perino *et al.*, 2019).

The Eurasian beaver (*Castor fiber*) is an exemplary case of a recovering mammal with multifaceted impacts on ecosystems and human activities. The beaver was once present in a large part of the Palearctic, from the western Iberian Peninsula to north-western China (Campbell-Palmer *et al.*, 2016; Halley, Saveljev, & Rosell, 2021). In Medieval times, this species underwent a severe decline due to the joint effects of habitat loss, hunting for fur, meat and the high request of 'castoreum', a fluid produced by the castor sacs (Halley & Rosell, 2002; Halley, Saveljev, & Rosell, 2021). In the early 20th century, the Eurasian beaver only survived in scattered refugia between France and Mongolia, hosting less than 1200 individuals. Since 1920, legal protection, together with reintroduction events and natural spread, triggered the recovery of the species in most of its original range, up to a current minimum population estimate of about 1.5 million individuals worldwide (Halley, Saveljev, & Rosell, 2021). Currently, the Eurasian beaver occurs with free-ranging and self-sustaining populations through most of its original range (apart from Portugal, UK and Southern Balkans), following both authorized and unauthorized releases (Halley, Saveljev, & Rosell, 2021; Kodzhabashev *et al.*, 2021; Calderón *et al.*, 2022; Mori *et al.*, 2022; Paladi & Cassir, 2022).

Beavers are ecosystem engineers that can improve the hydrogeological safety of rivers, increase local species richness and mitigate environmental pollution (Rosell *et al.*, 2005; Puttock *et al.*, 2017; Viviano *et al.*, 2022). The Eurasian beaver also represents an important keystone and umbrella species (Rosell *et al.*, 2005; Janiszewski, Hanzal, & Misiukiewicz, 2014) that builds habitat types for several other species, including the taxa of conservation concern (Dalbeck, Lüscher, & Ohlhoff, 2007; Nummi *et al.*, 2019; Viviano *et al.*, 2022). Additionally, this species is listed within the Annexes of the Habitats Directive (92/43/EEC), thus it is strictly protected and its range expansion requires careful monitoring (Genovesi *et al.*, 2014; Stoch & Genovesi, 2016). At the same time, the activity of beavers is known to greatly alter vegetation structure, in turn influencing other components of the ecosystems, including the diversity and abundance of invertebrates, amphibians and wading birds (Rosell *et al.*, 2005; Dalbeck, Lüscher, & Ohlhoff, 2007; Bashinskiy, 2020). Furthermore, beavers might damage tree plantations and artificial channels, leading to the risk of conflicts with humans (Swinnen *et al.*, 2017; Mikulka *et al.*, 2022a). Therefore, introductions and management efforts should be carefully planned in the light of interactions with human populations. In fact, both the International Union for Conservation of Nature and national authorities strongly discourage introductions or reintroductions conducted with no feasibility study and molecular/parasitological analyses (Kleiman, 1989). There is thus an urgent need to identify the areas where the beaver can expand, to target management and monitoring programmes.

In Italy, the beaver was present in central and northern regions in the Early Pleistocene, where it probably persisted in the eastern forests of the Po River lowland up to the 1500s (Pontarini, Lapini, & Molinari, 2019; Salari, Masseti, & Silvestri, 2020). Reintroduction programmes that occurred in the last century in neighbouring countries (Austria and Switzerland) between the 1970s and the 1990s have promoted the recolonization of many areas close to Italy (Halley, Saveljev, & Rosell, 2021). Starting in 2018, beavers also recolonized northern Italy, with multiple natural dispersal events from Austria (2019: Tarvisio, province of Udine; Pontarini, Lapini, & Molinari, 2019; 2020: Val Pusteria province of Bolzano). Subsequently, in March 2021, wildlife technicians and the members of the provincial police detected unequivocal signs of beaver presence in two areas of central Italy (Mori *et al.*, 2021; Pucci *et al.*, 2021). In the first area (Ombrone and Merse river basins), over 15 km of rivers were characterized by beaver presence; in the second one (Tevere River Basin), signs of beaver presence ran over >100 km (Mori *et al.*, 2021; Pucci *et al.*, 2021). These areas are extremely far from the forefront of the natural spread of the species (>400 km) and are separated from each other by >110 km in a straight line, thus suggesting at least two introduction events. In both areas, the reproduction of Eurasian beavers has been confirmed since at least 2021 (Mori *et al.*, 2022; Viviano *et al.*, 2022). Despite the importance of the Eurasian beaver as an ecosystem engineer and the complexity of its management, so far, areas of Italy that are actually suitable and likely to be colonized by this species are currently unknown (but see Serva, Biondi, & Iannella 2023 for a river-basin perspective).

Considering the high dispersal abilities of the Eurasian beaver (Campbell-Palmer *et al.*, 2016), species distribution models (SDMs; statistical models which estimate relationships between species occurrence and environmental characteristics) may represent a key tool to identify the areas where beaver expansion is most likely, both in Italy and in other areas of Europe. Additionally, connectivity models taking into account landscape resistance can help to identify the paths that will be most likely followed by a species expanding its range (McRae *et al.*, 2008; Dickson *et al.*, 2018). Such information is particularly important to target monitoring programmes and promote information campaigns that can limit conflicts with human populations. The implementation of SDM to achieve these tasks is not straightforward, as spatial autocorrelation, clustering and bias of occurrence data, and lack of occurrences in suitable areas where dispersal limitations have prevented re-colonization can bias the results of SDM, questioning the validity of model projections far from areas where occurrence data are available (Godsoe, 2010; Fourcade, Besnard, & Secondi, 2018; Ludwig *et al.*, 2023). Nevertheless, the use of appropriate validation can allow overcoming these limitations, leading to a robust identification of suitable areas for target species (Fourcade, Besnard, & Secondi, 2018; Valavi *et al.*, 2023).

Human–beaver conflict may arise in farmland areas, river areas dedicated to fishing and forest areas used for human activities (e.g. Verbeylen, 2003; Campbell-Palmer & Rosell, 2010; Siemer *et al.*, 2013; Mikulka *et al.*, 2022b). Therefore, predicting suitable areas for Eurasian beaver range expansion may help prevent conflicts with humans, indicating to wildlife managers how (and where) to set up actions to limit potential damages (Fidino *et al.*, 2022). The aim of our work is to identify the areas where beaver populations are most likely to be established in the near future within Europe, with a specific focus on Italy. First, we developed spatially cross-validated SDMs for Europe, to identify the areas with the highest suitability for the Eurasian beaver, and thus that might potentially sustain beaver populations. Second, we used connectivity modelling to assess the possible expansion routes of this species in Italy, to help environmental managers understand where to focus both future monitorings of beaver populations and actions to prevent and mitigate possible human–wildlife conflicts.

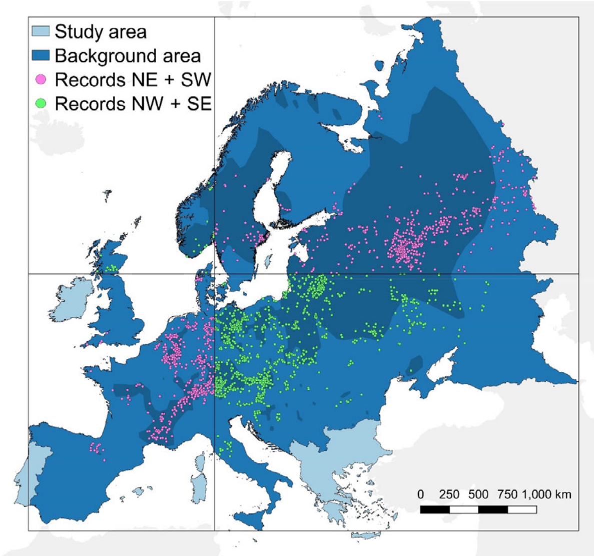

Figure 1 Map of the study area and Eurasian beaver occurrences used to model environmental suitability. The area used to randomly select background points for subsequent modelling is in blue. The four rectangles indicate the partial blocks used for spatial cross-validation. In order to perform spatial cross-validation, we divided the study area and the training points into two sets: north-east + south-west (NE + SW), in pink, and north-west + south-east (NW + SE), in green. Each model was trained with presence and background points from a given area and tested on the opposite area. The dark blue shaded areas represent the International Union for Conservation of Nature range (IUCN, 2008).

Materials and methods

Study area and occurrence records

The study area includes the European continent west of the Urals (Fig. 1), except for Iceland, where no historical information on beaver presence is available. We gathered Eurasian beaver occurrence records on 15 May 2023 from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/) and from the citizen-science platform iNaturalist (https://www.inaturalist.org/). We selected only records collected from 2005 (only research-grade records for iNaturalist) and with uncertainty <500 m, obtaining a total of 64 027 records for GBIF and 3742 records for iNaturalist. The dataset was integrated with 47 records collected in Italy by some of the authors through camera-trapping and visual search for presence signs (Mori *et al.*, 2021; Pucci *et al.*, 2021). Observations were projected to the European Terrestrial Reference System 1989 (ETRS89-extended/LAEA Europe; EPSG: 3035), which is appropriate for pan-European analyses. Only one record for each 1-km cell was kept, resulting in a total of 3412 unique records. In some areas (e.g. Austria and Belgium), beaver occurrences were much denser, probably because of a higher sampling effort. To limit the effects of unbalanced sampling and improve model transferability, occurrences were rarefied at a resolution of 10 km (Radosavljevic & Anderson, 2014; Aiello-Lammens *et al.*, 2015), resulting in a total of 1709 beaver occurrences used for subsequent modelling.

Species distribution models

The aim of this study was to assess suitability for the Eurasian beaver across the whole of Europe, including areas where beavers are currently extinct and dispersal constraints have so far prevented re-colonization. Several studies have questioned the reliability of predictions far beyond the location of training data (Ludwig *et al.*, 2023). Therefore, we modelled environmental suitability using an approach based on the use of spatially separated testing data, which enables robust spatial predictions (Radosavljevic & Anderson, 2014; Fourcade, Besnard, & Secondi, 2018; Valavi *et al.*, 2023). SDMs were built using Maxent, version 3.4.4 (Phillips, Dudík, & Schapire, 2017), which is among the modelling techniques with the best performance when the aim is predicting suitability outside the calibration area (Valavi *et al.*, 2023). The Maxent algorithm estimates the relationships between environmental predictors and species occurrence by minimizing the relative entropy in covariate space between probability densities of occurrence data and background data (i.e. the ratio between the two probability densities is estimated by choosing the probability density of occurrences that is most similar to the ones of backgrounds; Elith *et al.*, 2011; Merow, Smith, & Silander, 2013).

We adopted a three-step process: (1) we compared the performance of SDMs built with different sets of variables under a spatial cross-validation approach, in order to identify the combination of parameters producing the best spatial predictions; (2) we compared the performance of models with different complexity of species–environment relationships (regularization multiplier) to avoid overfitting and maximize predictive power; (3) lastly, we built a final model using the entire dataset of occurrences, the variable set selected at Step 1, and the regularization multiplier selected at Step 2.

We selected environmental predictors that are expected to have direct impacts on the Eurasian beavers, as they represent the occurrence of habitat (presence of rivers, slope, the percentage cover of deciduous or mixed deciduous–coniferous forests) or of suitable climatic conditions, including variables representing annual average and variation of temperatures, and annual amount and variation of precipitations (Dieter & McCabe, 1989; Fustec *et al.*, 2001; John, Baker, & Kostkan, 2010; Campbell *et al.*, 2012; Alakoski, Kauhala, & Selonen, 2019; a complete list of considered variables is available in Table S1). The river network was retrieved from Grill *et al.* (2019; available at: https://figshare.com/articles/dataset/Mapping_the_world_s_free-flowing_rivers_data_set_and_technical_documentation/7688801). Slope was derived from elevation data at 30′ resolution (~600 × 900 m in the centre of the study area) from the WorldClim dataset (version 2.1: Fick & Hijmans, 2017), using the 'terrain' function of the R package raster (Hijmans, 2022). Percentage cover of forests was derived from Tuanmu and Jetz (2014; available at EarthEnv: https://www.earthenv.org/landcover), by summing the percentage cover of the forest typologies most often used by beavers ('deciduous broadleaf trees' and 'mixed/other trees' [categories 3 and 4]; Hartman, 1996; Pinto, Santos, & Rosell, 2009). Climatic variables (Table S1) were retrieved from the CHELSA climatologies of the 1980–2010 period (version 2.1: Karger *et al.*, 2017). All maps were projected to the same coordinate reference system (EPSG: 3035) and converted to raster at a resolution of 1 × 1 km.

Step 1, selection of the best set of environmental variables: Spatial autocorrelation of distribution data and environmental predictors can severely bias the analysis of spatial data, undermining the validity of projections in distant areas (Dormann *et al.*, 2007; Veloz, 2009; Fourcade, Besnard, & Secondi, 2018). In order to identify the parameters yielding the best spatial predictions, we created 10 alternative sets of environmental variables (Table S1), keeping river presence, slope and forest cover in all sets, and changing the number and composition of climatic variables among sets. Strongly correlated variables ($r > |0.7|$) were not included in the same set (Table S2). Then, we adopted a spatial cross-validation approach to select the variables providing the highest power of predicting distribution (Radosavljevic & Anderson, 2014; Roberts *et al.*, 2017; Valavi *et al.*, 2023). We divided the study area into four blocks (Fig. 1) and, for each set of variables, we ran two models, using respectively north-eastern + south-western areas or south-eastern + north-western areas for model training (Fourcade, Besnard, & Secondi, 2018). Then, to choose the best-performing set of variables, we calculated the Continuous Boyce Index (CBI; Hirzel *et al.*, 2006), after projecting the models on the opposite areas (Valavi *et al.*, 2023). The CBI is a performance measure unrelated to species prevalence, hence it is appropriate to test the performance of models trained in different areas with potentially different species prevalence (Hirzel *et al.*, 2006). We calculated the CBI with the *ecospat* R package (Broennimann, Di Cola, & Guisan, 2023). For the selection of environmental variables, models were run using linear, quadratic and hinge features, with a regularization multiplier of 2. Regularization multiplier is a penalty given for each parameter included in the model and hence defines the model complexity (Warren & Seifert, 2011). A value of 2 has been suggested to provide a good compromise between fit to training data and the ability of extrapolation (Radosavljevic & Anderson, 2014; Ficetola *et al.*, 2020).

Step 2, selection of the best regularization multiplier: After selecting the best combination of predictors, we adopted the same spatial cross-validation approach to select the most appropriate regularization multiplier. We ran alternative models always using the best-performing set of variables while varying the regularization multiplier from 2 to 8 by steps of 1, as analyses performing cross-validation with truly independent data suggest that values below 2 can determine overfitted models, with low extrapolation capability (Moreno-Amat *et al.*, 2015). These models were trained on north-eastern + south-western areas or south-eastern + north-western areas and then validated on the opposite areas by calculating CBI (Fourcade, Besnard, & Secondi, 2018).

Step 3, final model: we ran a model trained on all the occurrences available in the selected training countries, using the best-performing regularization multiplier and combination of variables. The performance of this model was evaluated by calculating both the CBI and the area under the receiver operating characteristic curve (AUC) through a fivefold cross-validation, splitting the occurrences into five groups and running five different models using each time four groups for model training and one for testing. We evaluated the importance of variables through the permutation importance (PI) measure, which indicates the contribution of each variable to the Maxent model and is determined by calculating the train AUC decrease by performing random permutations of each given variable among training points. To confirm the robustness of the full model, the output and the response curves were compared with the sub-models calibrated on the different spatial blocks. All Maxent models were run from the R environment using the package *dismo* (Hijmans *et al.*, 2021), randomly sampling 100 000 background points (Figure S1) from the background area highlighted in Fig. 1.

Connectivity model

To evaluate the possible expansion routes of Eurasian beavers across Italy, we used the Circuitscape software to model structural connectivity (McRae *et al.*, 2008; Shah & McRae, 2008). This software applies the electric circuit theory in the field of ecology, to quantify the relative probability of movement of a species across a landscape. The landscape is viewed as an electrical circuit where each cell has a value of resistance (or its inverse, conductance), and where the current flows from sources (points of input of current) to grounds (points of arrival of current). We followed the framework developed by Falaschi *et al.* (2018) to evaluate the possible spread of Eurasian beavers in Italy. We selected as sources all the cells containing beaver occurrences in Italy and within a buffer of 50 km around Italy, and as grounds the borders of Italy plus the 50-km buffer. The conductance map was derived from the suitability map obtained from Maxent by: (i) rescaling all suitability values between 0–0.5 and 0–1000; (2) setting all cells with suitability >0.5 to a conductance value of 1000, as they are the cells with maximum suitability (Elith *et al.*, 2011); 3) setting all cells above 1800 m a.s.l. as not permeable (conductance of 0), given that high-altitude areas represent a physical barrier for beavers. Preliminary analysis with a range of alternative altitudinal limits provided nearly identical results. We ran Circuitscape in 'advanced' mode so that the current flows from sources to grounds (McRae, Shah, & Edelman, 2016). However, this mode prevents the current to flow from one source to another source. To avoid this repulsive effect and to evaluate the possible spread of Eurasian beavers in all directions, we ran Circuitscape from the R environment, where a separate connectivity model was carried out for each source point, and the resulting maps of current flow were summed (Falaschi *et al.*, 2018; Giuntini *et al.*, 2022; a tutorial and the data used to run the connectivity model are available at figshare: https://doi.org/10.6084/m9.figshare.24033489).

Identifying areas of potential human–beaver conflict

To better inform land managers and provide indication for focusing species monitoring, we identified areas where conflicts with humans are most likely to arise if beavers expand their range as predicted by suitability and connectivity models. In doing so, we selected areas of Italy with both high suitability and high structural connectivity (i.e. current flow estimated by the connectivity models). We chose a threshold of 0.344 for suitability, corresponding to the 10th percentile training presence, while for connectivity the threshold was 0.05, corresponding to the 5% of the current input used in connectivity modelling at each occurrence location. Within these areas, we defined possible categories of conflict at the 1-km resolution as follows: (1) presence of tree plantations, (2) presence of artificial channels and (3) presence of both the previous categories. Location of tree plantations was retrieved from Corine Land Cover of 2018 (European Environment Agency, 2020) and the presence of artificial channels was retrieved from the vector map of the hydrographic network of Italy (available at: http://www.pcn.minambiente.it/mattm/servizio-di-scaricamento-wfs/).

Results

Environmental suitability

The Maxent models used to select the most appropriate set of environmental variables showed very good performance, with CBI values from spatial cross-validation ranging from 0.903 to 0.990 (Table 1a). This indicates that the models calibrated with half of the data predict very well occurrences in the validation areas. The best-performing model included mean annual temperature (Bio1), mean monthly precipitation of the wettest quarter (Bio16) and mean monthly precipitation of the driest quarter (Bio17), plus river presence, slope and forest cover, which were kept in all models (Table 1).

Models for the selection of the regularization multiplier run with these six variables (Bio1, Bio16, Bio17, river presence, slope and forest cover) showed very good spatial cross-validation performance, with CBI values ranging from 0.799 to 0.996 (Table 1b). The final Maxent model was run with a regularization multiplier of 3, which was the one showing the best average cross-validation performance (Table 1b).

The final model showed a very good test CBI (0.945; SD = 0.010) and a test AUC of 0.791 (SD = 0.010). The most influential variables were mean annual temperature (PI = 50.4) and river presence (PI = 30), followed by precipitation of the wettest quarter (PI = 7.9), slope (PI = 5.5), forest cover (PI = 4.9) and precipitation of the driest quarter (PI = 1.2). Suitability showed a peak around a mean annual temperature of 5–11° (Figure S2). River presence showed a positive effect, with suitability increasing from ~0.45 to ~0.9 with the presence of a river in the cell (Fig. 2). Both precipitation variables (precipitation of the wettest/driest quarter) showed positive effects, indicating limited suitability in dry areas (Figure S2). Slope showed a strong negative effect, with suitability being the highest in flat terrains (Figure S2). While the effect of forest cover was weak, suitability was lower at extreme levels of forest cover (near 0% or 100%, Figure S2). Response curves were very consistent between the full model and the two spatially independent models (Figure S2), suggesting that the model provides a robust representation of relationships between the species and environmental variables.

Environmental suitability was generally high in central Europe, southern Scandinavia and Baltic countries (Fig. 2a). Unsuitable areas included the highest latitudes (above 60°N), the southern Iberian Peninsula and mountain chains such as the Alps and the Carpathians (Fig. 2a). In Italy, the highest suitability occurred in the foothills south of the Alps and in large parts of the Apennines (Fig. 2b). The eastern Po Plain (northern Italy), coastal areas and the islands showed low suitability (Fig. 2b).

Connectivity in Italy

The connectivity model showed a high potential for expansion from the records of central Italy to surrounding areas. These include not only regions where beavers are already widespread, such as Tuscany and Umbria, but also regions where the species is less common or so far absent, such as Emilia-Romagna, Marche, Lazio and Abruzzo (Fig. 3). Records of northern Italy seem to be more isolated. The current flow in the central and western regions of northern Italy was negligible, indicating that the central and western Alps can be a barrier to the expansion of beavers from France

Table 1 Performance of alternative Maxent models, calculated through spatial cross-validation and measured with Continuous Boyce Index (Hirzel *et al.*, 2006)

(a)

Bioclimatic variables	Continuous Boyce Index – NESW	Continuous Boyce Index – NWSE	Mean Continuous Boyce Index
Bio1, Bio4, Bio12, Bio15	0.977	0.953	0.965
Bio1, Bio4, Bio16, Bio17	0.922	0.949	0.936
Bio1, Bio7, Bio12, Bio15	0.990	0.918	0.954
Bio1, Bio7, Bio16, Bio17	0.917	0.935	0.926
Bio1, Bio12	0.956	0.971	0.964
Bio1, Bio16, Bio17	**0.981**	**0.974**	**0.978**
Bio5, Bio6, Bio12, Bio15	0.974	0.977	0.976
Bio5, Bio6, Bio16, Bio17	0.925	0.940	0.933
Bio1, Bio7	0.903	0.936	0.920
Bio1, Bio7, Bio12	0.989	0.928	0.959

(b)

Regularization multiplier	Continuous Boyce Index – NESW	Continuous Boyce Index – NWSE	Mean Continuous Boyce Index
2	0.985	0.977	0.981
3	**0.978**	**0.985**	**0.982**
4	0.906	0.980	0.943
5	0.895	0.990	0.943
6	0.817	0.986	0.902
7	0.799	0.996	0.898
8	0.800	0.975	0.888

(a) Modelling Step 1 (see Section 2): Performance of models run to select the most appropriate set of variables. Besides climatic variables, all alternative models included river presence, slope and forest cover. (b) Modelling Step 2 (the set of climatic variables used in Step 2 is the one in bold in a): Performance of models run with alternative regularization multipliers. Bio1: mean annual temperature; Bio4: temperature seasonality; Bio5: mean temperature of the warmest month; Bio6: mean temperature of the coldest month; Bio7: annual temperature range; Bio12: annual precipitation; Bio15: precipitation seasonality; Bio16: mean monthly precipitation of the wettest quarter; Bio17: mean monthly precipitation of the driest quarter. Best models are highlighted in bold.

and Switzerland. While the current flow across north-eastern regions was lower compared to that in central Italy, some possible expansion routes occurred in the Trentino-Alto Adige, Veneto and Friuli Venezia Giulia regions (Fig. 3). A high current flow is present between beaver populations of eastern Austria and both areas of occurrence in Italy (Val Pusteria in Trentino-Alto Adige and Tarvisio in Friuli Venezia Giulia). High current flow also occurred between the records of Alto Adige (Val Pusteria), and beaver records of the Innsbruck area in western Austria (Fig. 3), suggesting a possible connection through the valleys of the Isarco and Rienza rivers.

Areas of potential human–beaver conflict

The main areas of potential human–beaver conflicts are in the north-eastern regions (Trentino-Alto Adige and Friuli-Venezia Giulia; Fig. 4b) and in central Italy (Emilia-Romagna, Tuscany, Umbria, Marche, and Lazio regions; Fig. 4c). Most of the highlighted areas included the presence of tree plantations, while only a few areas included artificial channels, particularly in central Trentino-Alto Adige and eastern Tuscany.

Discussion

After centuries of persecution by humans, conservation efforts and legal protection jointly allowed Eurasian beavers to reconquer most of their previous range in Europe (Halley, Saveljev, & Rosell, 2021; Kodzhabashev *et al.*, 2021; Calderón *et al.*, 2022; Paladi & Cassir, 2022). While rewilding projects can have strong positive effects on biodiversity conservation and human health (Cerqueira *et al.*, 2015), the reintroduction of ecosystem engineers such as beavers may cause conflicts with human activities (Swinnen *et al.*, 2017; Auster, Barr, & Brazier, 2020; Auster, Puttock, & Brazier, 2020). By performing spatially cross-validated SDMs coupled with connectivity models, we highlighted suitable areas for the Eurasian beaver across Europe and identified possible expansion routes and conflict areas in Italy, a country recently re-colonized by this species due to both natural expansion and illegal reintroductions.

Environmental suitability in Europe and Italy

Human activities and climate change have deeply altered river flow and the structure of many lowland riparian forests (Nilsson & Berggren, 2000; Slezák *et al.*, 2022), implying that current habitat suitability for beavers might be largely different after centuries of absence in certain areas. However, our model generally showed high suitability over broad parts of the historical distribution range, including areas where beavers have been extirpated (Fig. 1: Halley, Saveljev, & Rosell, 2021). The highest suitability was found in central

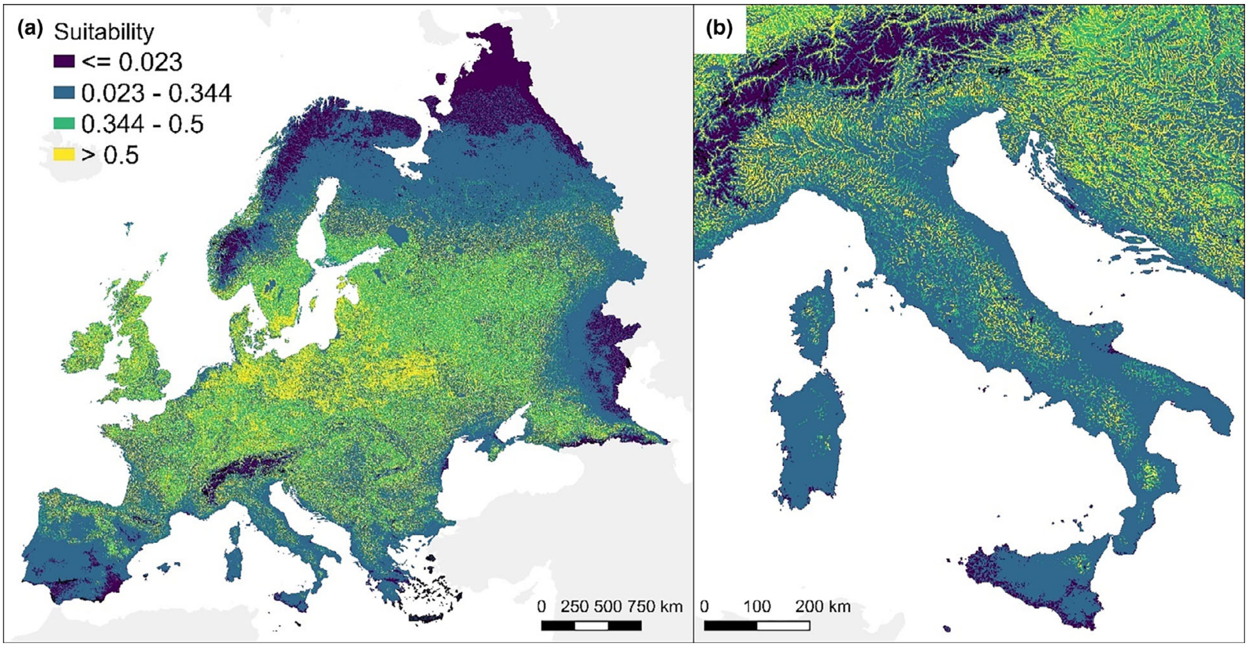

Figure 2 Environmental suitability for the Eurasian beaver across Europe (a) and Italy (b), as predicted by the Maxent model. The thresholds of 0.023 and 0.344, respectively, indicate the minimum training presence and the 10th percentile training presence.

and eastern Europe, where most beavers actually occur (Halley, Saveljev, & Rosell, 2021; Kodzhabashev *et al.*, 2021; Paladi & Cassir, 2022). Boreal landscapes include many beaver refugia and currently host increasing beaver populations occupying both optimal (meandering streams with the occurrence of grass and forbs on the ground) and marginal habitats (Hartman, 1996; Pinto, Santos, & Rosell, 2009; Halley, Saveljev, & Rosell, 2021). In the northernmost countries, suitability was high in southern Scandinavia, whereas cold temperatures limit the distribution of this species at the highest latitudes, as well as in high mountain ecosystems of central and southern Europe (Fig. 2). In fact, ice and snow cover over long periods may limit the use of water by beavers; furthermore, in high mountains, the fast stream flow limits the stability of dams and lodges, thus reducing beaver establishment (Bylak, Kukuła, & Mitka, 2014; Giriat, Gorczyca, & Sobucki, 2016; Smeraldo *et al.*, 2017; Bartra Cabre *et al.*, 2020; Wojton & Kukuła, 2021). Unsuitable areas also included xeric areas of Southern Europe, such as the southern Iberian Peninsula and most coastal Mediterranean areas (Fig. 2). Beavers are semi-aquatic rodents that need water throughout the year; feeding and other activity mostly occurs within 20 m of the water edge (Gaywood, 2018). Therefore, severe droughts in warm months as those occurring in southern Europe are major limiting factors (Zavyalov *et al.*, 2015; Oikonomou *et al.*, 2020; Sutanto *et al.*, 2020; Serva, Biondi, & Iannella, 2023). Similarly, in Italy, suitability was low in areas with cold climates (e.g. the Alps) or with warm and dry Mediterranean climates (e.g. southernmost regions; Fig. 2b). Northern regions of Italy showed a medium to high suitability for beavers, confirming the outputs by Treves *et al.* (2020, 2022), who showed high suitability for Eurasian beavers in western and southern Piedmont at intermediate altitudes. Our model, instead, suggested a low suitability for beavers in the eastern Po plain. In this area, human activities have deeply altered and fragmented the natural river flow, limiting the cover of riparian woodland and, thus, reducing resources and habitats for beavers (Marchetti, 2002; Poldini *et al.*, 2020). Conversely, large parts of the Apennines, including the areas of central Italy where reproductive populations occur (Mori *et al.*, 2022), showed high suitability (Fig. 2b). Central Italy is largely covered with natural vegetation and harbours many rivers still surrounded by riparian forests, thus providing optimal habitats for beaver reproduction (Lastrucci, Paci, & Raffaelli, 2010; Baiocchi *et al.*, 2012; Sensi *et al.*, 2020). Low beaver population densities, such as the one observed in central Italy, together with suitable habitats, may trigger rapid population expansion of this rodent (Wróbel, 2020).

Connectivity and potential expansion in Italy

Connectivity modelling showed a negligible flow of current in north-western and southernmost Italian regions (Fig. 3). Beaver records of France and Switzerland were completely isolated from Italy, supporting the role of the western Alps as barriers for the recolonization of Italy. The higher current flow occurring in north-eastern Italy provides further support to the hypothesis that beavers in north-eastern Italy arrived through natural expansion (Loy *et al.*, 2019; Pontarini, Lapini, & Molinari, 2019). While the most likely route for

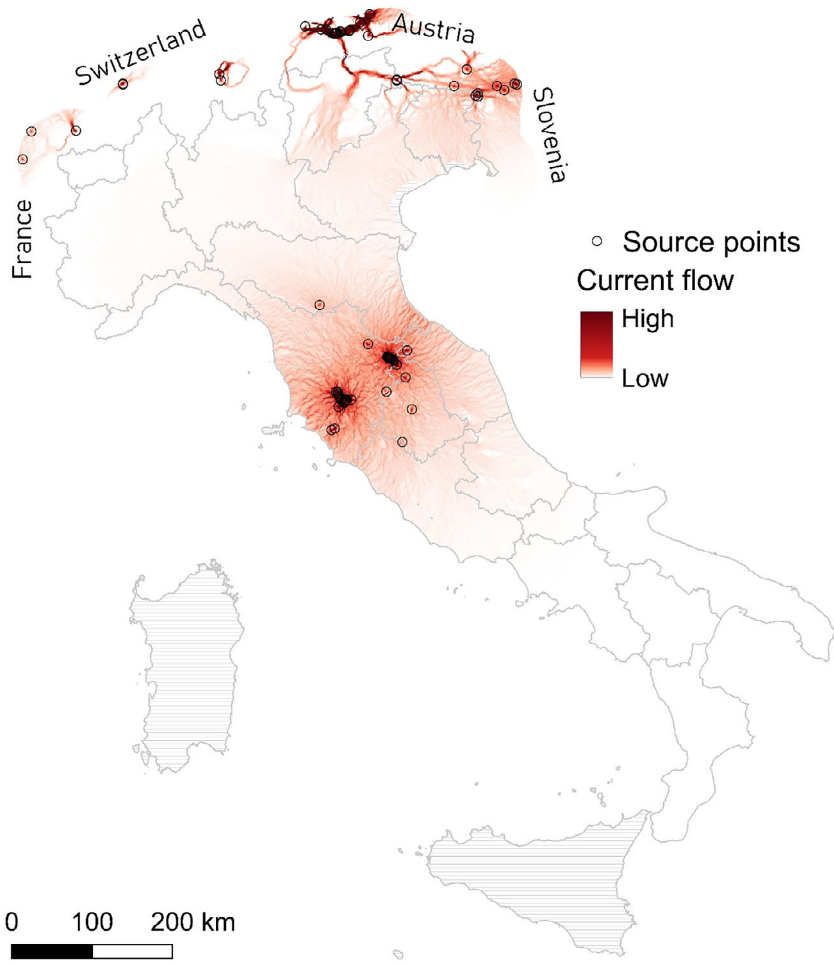

Figure 3 Connectivity map of Eurasian beaver in Italy and surrounding countries. Black circles represent source points (beaver occurrences) while the current flow is represented in red.

recolonization of northern Italy may occur between Austria and north-eastern Italian regions, the intense urbanization of many river valleys might act as a barrier for beaver dispersal. The flow between central and north-eastern Italy was nearly zero, confirming that the natural dispersal between these areas is unlikely, and unauthorized translocations are the most likely source of these populations. Nevertheless, connectivity was high within central Italy, suggesting a high potential for expansion into the surrounding regions. Given the extent of beaver distribution in central Italy, the generally high suitability and the lack of major barriers, we expect a rapid expansion over the Apennines in the absence of direct management interventions, as suggested for similar areas (Wróbel, 2020).

Study limitations

The use of connectivity models for conservation purposes has provided reliable results in the last two decades (Chetkiewicz, St Clair, & Boyce, 2006; Giuntini *et al.*, 2022). On the one hand, our estimates of connectivity might underestimate the potential spread of beavers in Italy, given that they may also disperse through unsuitable landscape matrix (Vanstaen, 2019) or through human-mediated translocations (Calderón *et al.*, 2022). On the other hand, some fine-scale landscape elements not mapped in our analysis, such as artificial dams or other infrastructures, might limit beaver movements. Additionally, our model does not provide a temporal framework for the expansion, but future studies can integrate multi-temporal data with connectivity and suitability values to provide an estimate of beaver expansion through time in the absence of management (Ficetola *et al.*, 2010). However, these studies would require precise and long-term data on beaver expansion.

Conservation implications and human–beaver conflicts

Despite some limitations, SDMs and connectivity models can provide useful information for ad hoc monitoring and early detection of species expanding their ranges. Robust models with strong spatial validation, as the ones shown in

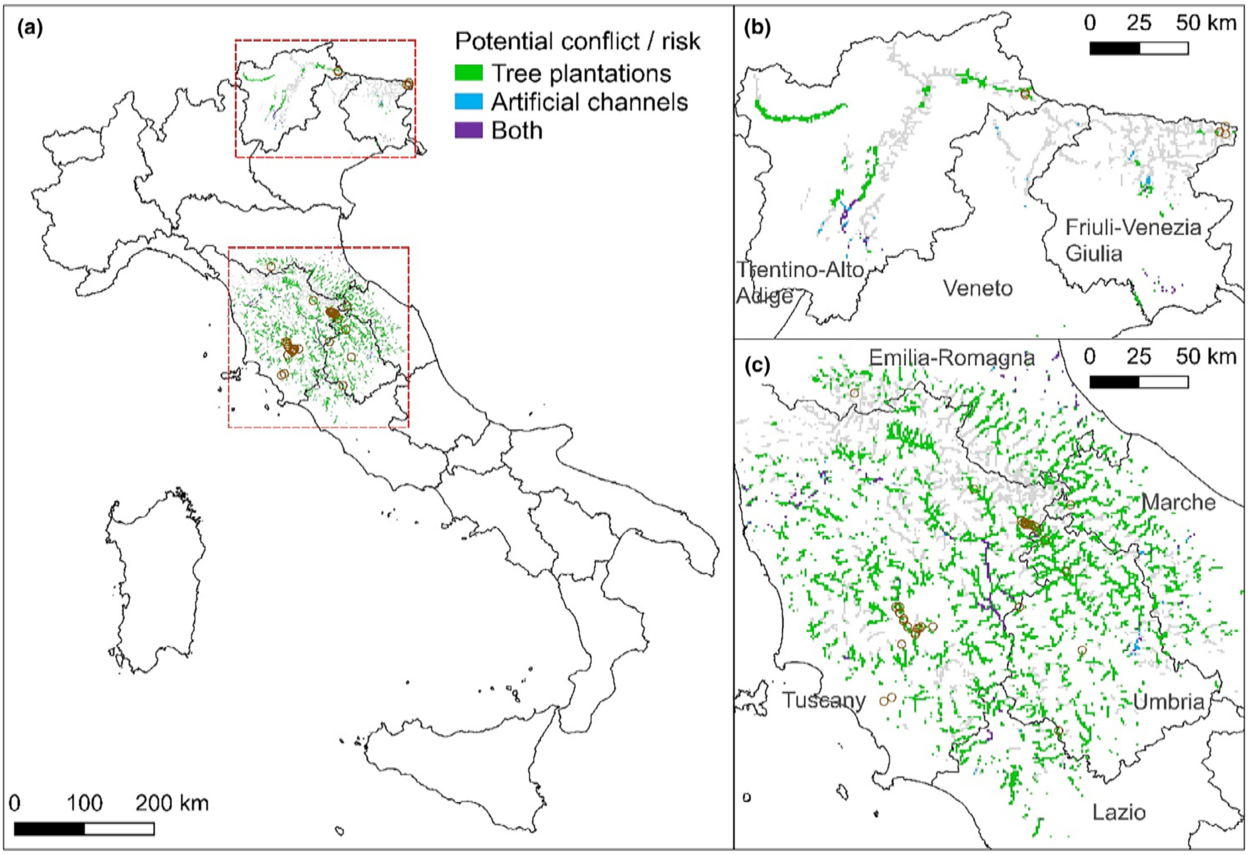

Figure 4 Areas of potential human–beaver conflict. Cells of the study area of both high suitability, as estimated by the species distribution model (> of 10th percentile training presence), and high current flow, as estimated by the connectivity model (> of the 5% of the input current), are in grey. Within these cells, we highlight areas including tree plantations (green), artificial channels (blue) and both (violet). Brown circles are beaver occurrences used for connectivity modelling. Two main areas of potential conflicts are evident: north-eastern regions (panel b) and central Italy (panel c).

this work, may provide reliable predictions of species expansion, enabling the identification of suitable areas where to concentrate monitoring, prevention and conservation efforts (Fig. 4). This is pivotal in the case of the Eurasian beaver since this ecosystem engineer can deeply modify environments, potentially causing conflicts with human activities (Brazier *et al*., 2021). For instance, wood cutting and dam-/lodge-building activities by beavers can have disproportionate effects on ecosystem structure and function compared to beaver abundance and biomass (Janiszewski, Hanzal, & Misiukiewicz, 2014). By creating new lentic microhabitats, beaver establishment can foster the colonization and persistence of some protected species, including threatened vertebrates and invertebrates (Dalbeck, Lüscher, & Ohlhoff, 2007; Stoch & Genovesi, 2016; Orazi *et al*., 2022; Viviano *et al*., 2022). Furthermore, the presence of beaver may facilitate numerical control towards the invasive coypu (*Myocastor coypus*), by forcing coypus to increase activity in diurnal hours, possibly providing more encounters with humans (Mori *et al*., 2022). Monitoring freshwater habitats in areas that are likely to be colonized by beavers is essential to record local biodiversity changes and take advantage of these novel conservation opportunities.

Conflicts with human activities are also possible (Siemer *et al*., 2013). While several authors suggest that beavers may limit flood risk by creating dams and lodges that attenuate river flowing (Puttock *et al*., 2021; Ronnquist & Westbrook, 2021), the modification of water flow poses challenges when the redirection of water alters artificial water supply in agricultural landscapes or damages human infrastructures in suburban areas (Campbell-Palmer *et al*., 2016; Jackowiak, Busher, & Krauze-Gryz, 2020). For these reasons, the possible consequences of beaver translocations and expansion should be always carefully evaluated. For instance, the appropriate management of productive and human-dominated landscapes can be implemented in some areas identified by our spatial analyses (Fig. 4), such as protection of agricultural fields with fences and drainage of wetlands threatening human infrastructures (cf. Parker & Rosell, 2003; Auster, Barr, & Brazier, 2021). In north-eastern Italy, our analyses suggest limited conflicts in Friuli-Venezia Giulia, where beavers are likely to expand mostly in unmanaged landscapes, while impacts may be higher in Trentino-Alto Adige, where beavers can have access to areas where tree plantations and human infrastructures are more prevalent (Fig. 4b). Similarly, in central Italy, beavers may expand into areas where tree plantations occur (Fig. 4c). Even if no serious damage or conflict has been reported yet (Kloskowski, 2011; Mikulka *et al*., 2020), we advocate increased monitoring and/or structural measures at critical locations (Fig. 4) to prevent conflicts between beavers and human activities. In fact, the long-term coexistence between humans and beavers can be achieved by preventing or quickly resolving human–wildlife conflicts, thus avoiding drastic measures (Swinnen *et al*., 2017). Effective and cheap non-lethal methods of damage control can be employed following methods applied in Norway, that is by limiting access to crops by beavers through solid fences in areas of potential expansion (Parker & Rosell, 2003). Finally, adequate monitoring and stakeholder involvement through education campaigns can boost the implementation of these measures, preventing human–beaver conflicts for peaceful coexistence and positive effects on biodiversity.

Acknowledgements

The authors would like to thank all volunteers who helped in field data collection, in particular Chiara Pucci and Davide Senserini, who triggered the research line on Eurasian beavers in central Italy. Beaver monitoring in central Italy was funded by the Beaver Trust, UK (grant number: 1185451), and by WWF Italia (Prot. 0261766708092023 UOR: 532). EM and GM were funded by the National Recovery and Resilience Plan (NRRP), Mission 4 Component 2 Investment 1.4 – Call for Tender No. 3138 of 16 December 2021, rectified by Decree n.3175 of 18 December 2021 of the Italian Ministry of University and research funded by the European Union – NextGenerationEU; Project code CN_00000033, Concession Decree No. 1034 of 17 June 2022 adopted by the Italian Ministry of University and Research, CUP B83C22002930006, Project title 'National Biodiversity Future Center – NBFC'. The comments of two reviewers greatly improved a previous draft of this paper.

Author contributions

MF, GFF and EM conceived the ideas and led the writing of the paper; AV, GM and EM collected the data; MF and GFF analyzed the data. All authors gave final approval for publication.

Conflicts of interest

The authors declare that there are no conflicts of interest.

Data availability statement

The maps presented in this paper (suitability, connectivity and conflict), together with a tutorial to run Circuitscape 4.0 from R with customized functions, are available at figshare: https://doi.org/10.6084/m9.figshare.24033489.

References

Aiello-Lammens, M.E., Boria, R.A., Radosavljevic, A., Vilela, B. & Anderson, R.P. (2015). spThin: an R package for spatial thinning of species occurrence records for use in ecological niche models. *Ecography* **38**, 541–545.

Alakoski, R., Kauhala, K. & Selonen, V. (2019). Differences in habitat use between the native Eurasian beaver and the invasive North American beaver in Finland. *Biol. Invasions* **21**, 1601–1613.

Auster, R.E., Barr, S.W. & Brazier, R.E. (2020). Wildlife tourism in reintroduction projects: exploring social and economic benefits of beaver in local settings. *J. Nat. Conserv.* **58**, 125920.

Auster, R.E., Barr, S.W. & Brazier, R.E. (2021). Improving engagement in managing reintroduction conflicts: learning from beaver reintroduction. *J. Environ. Plann. Manag.* **64**, 1713–1734.

Auster, R.E., Puttock, A. & Brazier, R. (2020). Unravelling perceptions of Eurasian beaver reintroduction in Great Britain. *Area*, **52**, 364–375.

Baiocchi, S., Fattorini, S., Bonavita, P. & Vigna Taglianti, A. (2012). Patterns of beta diversity in riparian ground beetle assemblages (Coleoptera Carabidae): a case study in the River Aniene (Central Italy). *Ital. J. Zool.* **79**, 136–150.

Bartra Cabre, L., Mayer, M., Steyaert, S. & Rosell, F. (2020). Beaver (*Castor fiber*) activity and spatial movement in response to light and weather conditions. *Mammal. Biol.* **100**, 261–271.

Bashinskiy, I.V. (2020). Beavers in lakes: a review of their ecosystem impact. *Aquat. Ecol.* **54**, 1097–1120.

Brazier, R.E., Puttock, A., Graham, H.A., Auster, R.E., Davies, K.H. & Brown, C.M. (2021). Beaver: nature's ecosystem engineers. *Wiley Interdiscip. Rev. Water* **8**, e1494.

Broennimann, O., Di Cola, V. & Guisan, A. (2023). ecospat: spatial ecology miscellaneous methods. R package version 3.5. https://CRAN.R-project.org/package=ecospat

Bylak, A., Kukuła, K. & Mitka, J. (2014). Beaver impact on stream fish life histories: the role of landscape and local attributes. *Can. J. Fish. Aquat. Sci.* **71**, 1603–1615.

Calderón, T., Balmori-de la Puente, A., Caballero, J.M., Rodríguez, D., Caballero, A. & Balmori, A. (2022). The Eurasian beaver in the western Iberian Peninsula. *Hystrix* **33**, 213–215.

Campbell, R.D., Nouvellet, P., Newman, C., Macdonald, D.W. & Rosell, F. (2012). The influence of mean climate trends and climate variance on beaver survival and recruitment dynamics. *Glob. Chang. Biol.* **18**, 2730–2742.

Campbell-Palmer, R., Jones, S., Parker, H., Rosell, F., Gow, D., Schwab, G. & Dickinson, H. (2016). *The Eurasian beaver handbook: ecology and management of Castor fiber.* London, UK: Pelagic Publishing Ltd.

Campbell-Palmer, R. & Rosell, F. (2010). Conservation of the Eurasian beaver *Castor fiber*: an olfactory perspective. *Mamm. Rev.* **40**, 293–312.

Cerqueira, Y., Navarro, L.M., Maes, J., Marta-Pedroso, C., Pradinho Honrado, J. & Pereira, H.M. (2015). Ecosystem services: the opportunities of rewilding in Europe. In *Rewilding European landscapes*: 47–64. Pereira, H.M. & Navarro, L.M. (Eds). New York, USA: Springer Editions.

Chapron, G., Kaczensky, P., Linnell, J.D., Von Arx, M., Huber, D., Andrén, H. & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science* **346**, 1517–1519.

Chetkiewicz, C.B., St Clair, C.C. & Boyce, M.S. (2006). Corridors for conservation: integrating pattern and process. *Annu. Rev. Ecol. Evol. Syst.* **37**, 317–342.

Cimatti, M., Ranc, N., Benítez-López, A., Maiorano, L., Boitani, L., Cagnacci, F., Čengić, M., Ciucci, P., Huijbregts, M.A.J., Krofel, M., López-Bao, J.V., Selva, N., Andren, H., Bautista, C., Ćirović, D., Hemmingmoore, H., Reinhardt, I., Marenče, M., Mertzanis, Y., Pedrotti, L., Trbojević, I., Zetterberg, A., Zwijacz-Kozica, T. & Santini, L. (2021). Large carnivore expansion in Europe is associated with human population density and land cover changes. *Divers. Distrib.* **27**, 602–617.

Dalbeck, L., Lüscher, B. & Ohlhoff, D. (2007). Beaver ponds as habitat of amphibian communities in a central European highland. *Amphib.-Reptil.* **28**, 493–501.

Deinet, S., Ieronymidou, C., McRae, L., Burfield, I.J., Foppen, R.P.B., Collen, B. & Böhm, M. (2013). *Wildlife comeback to Europe: the recovery of selected mammal and bird species*. London, UK: ZSL.

Dickson, B.G., Albano, C.M., Gray, M.E., McClure, M.L., Theobald, D.M., Anantharaman, R., Shah, V.B., Beier, P., Fargione, J., Hall, K.R., Graves, T.A., Lawler, J.J., Leonard, P.B., Littlefield, C.E., Novembre, J., Schloss, C.A., Schumaker, N.H., Gray, M.E., Shah, V.B. & Theobald, D.M. (2018). Circuit-theory applications to connectivity science and conservation. *Conserv. Biol.* **33**, 239–249.

Dieter, C.D. & McCabe, T.R. (1989). Factors influencing beaver lodge-site selection on a prairie river. *Am. Midl. Nat.* **122**, 408–411.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007). Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* **30**, 609–628.

Elith, J., Phillips, S.J., Hastie, T., Dudík, M., Chee, Y.E. & Yates, C.J. (2011). A statistical explanation of MaxEnt for ecologists. *Divers. Distrib.* **17**, 43–57.

European Environment Agency. (2020). Corine Land Cover (CLC) 2018, version V2020_v20u1. Available at: https://land.copernicus.eu/pan-european/corine-land-cover/clc2018?tab=download. Accessed on 12 February 2023.

Falaschi, M., Mangiacotti, M., Sacchi, R., Scali, S. & Razzetti, E. (2018). Electric circuit theory applied to alien invasions: a connectivity model predicting the Balkan frog expansion in northern Italy. *Acta Herpetol.* **13**, 33–42.

Ficetola, G.F., Bonardi, A., Mairota, P., Leronni, V. & Padoa-Schioppa, E. (2014). Predicting wild boar damages to croplands in a mosaic of agricultural and natural areas. *Curr. Zool.* **60**, 170–179.

Ficetola, G.F., Fanelli, M., Garizio, L., Falaschi, M., Tenan, S., Ghielmi, S., Laddaga, L., Menegon, M. & Delfino, M. (2020). Estimating abundance and habitat suitability in a micro-endemic snake: the Walser viper. *Acta Herpetol.* **15**, 73–85.

Ficetola, G.F., Maiorano, L., Falcucci, A., Dendoncker, N., Boitani, L., Padoa-Schioppa, E., Miaud, C. & Thuiller, W. (2010). Knowing the past to predict the future: land-use change and the distribution of invasive bullfrogs. *Glob. Chang. Biol.* **16**, 528–537.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315.

Fidino, M., Lehrer, E.W., Kay, C.A., Yarmey, N.T., Murray, M.H., Fake, K., Adams, H.C. & Magle, S.B. (2022). Integrated species distribution models reveal spatiotemporal patterns of human–wildlife conflict. *Ecol. Appl.* **32**, e2647.

Fourcade, Y., Besnard, A.G. & Secondi, J. (2018). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Glob. Ecol. Biogeogr.* **27**, 245–256.

Fustec, J., Lodé, T., Le Jacques, D. & Cormier, J.P. (2001). Colonization, riparian habitat selection and home range size in a reintroduced population of European beavers in the Loire. *Freshw. Biol.* **46**, 1361–1371.

Gaywood, M.J. (2018). Reintroducing the Eurasian beaver *Castor fiber* to Scotland. *Mamm. Rev.* **48**, 48–61.

Genovesi, P., Angelini, P., Duprè, E., Ercole, S., Giacanelli, V., Ronchi, F. & Stoch, F. (2014). Specie ed habitat di interesse comunitario in Italia: distribuzione, stato di conservazione e trend. ISPRA, Serie Rapporti, 194/2014.

Giriat, D., Gorczyca, E. & Sobucki, M. (2016). Beaver ponds' impact on fluvial processes (Beskid Niski Mts., SE Poland). *Sci. Total Environ.* **544**, 339–353.

Giuntini, S., Ancillotto, L., Falaschi, M., Viviano, A., Palagi, E. & Mori, E. (2022). Alien parakeets as a potential threat to the common noctule *Nyctalus noctula*. *Biodivers. Conserv.* **31**, 3075–3092.

Godsoe, W. (2010). I can't define the niche but I know it when I see it: a formal link between statistical theory and the ecological niche. *Oikos* **119**, 53–60.

Grill, G., Lehner, B., Thieme, M., Geenen, B., Tickner, D., Antonelli, F., Babu, S. et al. (2019). Mapping the world's free-flowing rivers. *Nature* **569**, 215–221.

Halley, D.J. & Rosell, F. (2002). The beaver's reconquest of Eurasia: status, population development, and management of a conservation success. *Mamm. Rev.* **32**, 153–178.

Halley, D.J., Saveljev, A.P. & Rosell, F. (2021). Population and distribution of beavers *Castor fiber* and *Castor canadensis* in Eurasia. *Mamm. Rev.* **51**, 1–24.
Hartman, G. (1996). Habitat selection by European beaver (*Castor fiber*) colonizing a boreal landscape. *J. Zool.* **240**, 317–325.
Higgins, P.A. (2007). Biodiversity loss under existing land use and climate change: an illustration using northern South America. *Glob. Ecol. Biogeogr.* **16**, 197–204.
Hijmans, R.J. (2022). raster: geographic data analysis and modeling. R Package version 3.5-15. Available at https://rspatial.github.io/raster/index.html
Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2021). dismo: species distribution modeling. R package version 1.3-5. https://CRAN.R-project.org/package=dismo
Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecol. Model.* **199**, 142–152.
IUCN (International Union for Conservation of Nature). (2008). *Castor fiber*. The IUCN Red List of Threatened Species. Version 2022-2. https://www.iucnredlist.org Downloaded on 29 May 2023.
Jackowiak, M., Busher, P. & Krauze-Gryz, D. (2020). Eurasian beaver (*Castor fiber*) winter foraging preferences in Northern Poland—The role of woody vegetation composition and anthropopression level. *Animals* **10**, 1376.
Janiszewski, P., Hanzal, V. & Misiukiewicz, W. (2014). The Eurasian beaver (*Castor fiber*) as a keystone species–a literature review. *Balt. For.* **20**, 277–286.
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.
Karger, D.N., Conrad, O., Böhner, J., Kawohl, T., Kreft, H., Soria-Auza, R.W., Zimmermann, N.E., Linder, H.P. & Kessler, M. (2017). Climatologies at high resolution for the earth's land surface areas. *Sci. Data* **4**, 170122.
Kleiman, D.G. (1989). Reintroduction of captive mammals for conservation. *Bioscience* **39**, 152–161.
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.
Kodzhabashev, N.D., Tsvyatkova, D.D., Krastev, K.V., Ignatov, M.M. & Teofilova, T.M. (2021). The Eurasian beaver *Castor fiber* Linnaeus, 1758 (Rodentia: Castoridae) is returning to Bulgaria. *Acta Zool. Bulg.* **73**, 587–595.
Lastrucci, L., Paci, F. & Raffaelli, M. (2010). The wetland vegetation of the Natural Reserves and neighbouring stretches of the Arno river in the Arezzo province (Tuscany, Central Italy). *Fitosociologia* **47**, 31–61.
Loy, A., Aloise, G., Ancillotto, L., Angelici, F.M., Bertolino, S., Capizzi, D., Castiglia, R., Colangelo, P., Contoli, L., Cozzi, B., Fontaneto, D., Lapini, L., Maio, N., Monaco, A., Mori, E., Nappi, A., Podestà, M., Russo, D., Sarà, M., Scandura, M. & Amori, G. (2019). Mammals of Italy: an annotated checklist. *Hystrix* **30**, 87–106.
Ludwig, M., Moreno-Martinez, A., Hölzel, N., Pebesma, E. & Meyer, H. (2023). Assessing and improving the transferability of current global spatial prediction models. *Glob. Ecol. Biogeogr.* **32**, 356–368.
Marchetti, M. (2002). Environmental changes in the Central Po plain (northern Italy) due to fluvial modifications and anthropogenic activities. *Geomorphology* **44**, 361–373.
Marta, S., Brunetti, M., Manenti, R., Provenzale, A. & Ficetola, G.F. (2021). Climate and land-use changes drive biodiversity turnover in arthropod assemblages over 150 years. *Nat. Ecol. Evol.* **5**, 1291–1300.
McRae, B.H., Dickson, B.G., Keitt, T.H. & Shah, V.B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology* **89**, 2712–2724.
McRae, B.H., Shah, V.B. & Edelman, A. (2016). Circuitscape: modeling landscape connectivity to promote conservation and human health. *Nat. Conserv.* **14**, 1–14.
Merow, C., Smith, M.J. & Silander, J.A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography* **36**, 1058–1069.
Mikulka, O., Adamec, Z., Kamler, J., Homolka, M., Drimaj, J., Plhal, R. & Petr, P. (2022*b*). Using deciduous softwoods to protect commercial forest stands against damage by Eurasian beaver (*Castor fiber* L.). *For. Ecol. Manag.* **520**, 120328.
Mikulka, O., Homolka, M., Drimaj, J. & Kamler, J. (2020). European beaver (*Castor fiber*) in open agricultural landscapes: crop grazing and the potential for economic damage. *Eur. J. Wildl. Res.* **66**, 101.
Mikulka, O., Pyszko, P., Skoták, V., Kamler, J., Drimaj, J., Plhal, R. & Homolka, M. (2022*a*). The influence of forestry management on the selection of a non-vegetative diet by the Eurasian beaver (*Castor fiber* L.). *Animals* **12**, 2949.
Moreno-Amat, E., Mateo, R.G., Nieto-Lugilde, D., Morueta-Holme, N., Svenning, J.C. & García-Amorena, I. (2015). Impact of model complexity on cross-temporal transferability in Maxent species distribution models: an assessment using paleobotanical data. *Ecol. Model.* **312**, 308–317.
Mori, E., Mazza, G., Pucci, C., Senserini, D., Campbell-Palmer, R., Contaldo, M. & Viviano, A. (2022). Temporal activity patterns of the Eurasian beaver and coexisting species in a Mediterranean ecosystem. *Animals* **12**, 1961.
Mori, E., Viviano, A., Brustenga, L., Olivetti, F., Peppucci, L., Pucci, C., Senserini, D., Sergiacomi, U., Spilinga, C., Roversi, P.F. & Mazza, G. (2021). Distribution and genetic analysis of wild-living Eurasian beavers in Central Italy. *Redia* **104**, 209–215.
Moseby, K.E., Lollback, G.W. & Lynch, C.E. (2018). Too much of a good thing; successful reintroduction leads to overpopulation in a threatened mammal. *Biol. Conserv.* **219**, 78–88.
Nawaz, M.A., Swenson, J.E. & Zakaria, V. (2008). Pragmatic management increases a flagship species, the Himalayan

brown bears, in Pakistan's Deosai National Park. *Biol. Conserv.* **141**, 2230–2241.

Nilsson, C. & Berggren, K. (2000). Alterations of riparian ecosystems caused by river regulation: dam operations have caused global-scale ecological changes in riparian ecosystems. How to protect river environments and human needs of rivers remains one of the most important questions of our time. *Bioscience* **50**, 783–792.

Nummi, P., Liao, W., Huet, O., Scarpulla, E. & Sundell, J. (2019). The beaver facilitates species richness and abundance of terrestrial and semi-aquatic mammals. *Glob. Ecol. Conserv.* **20**, e00701.

Oikonomou, P.D., Karavitis, C.A., Tsesmelis, D.E., Kolokytha, E. & Maia, R. (2020). Drought characteristics assessment in Europe over the past 50 years. *Water Resour. Manag.* **34**, 4757–4772.

Orazi, V., Hagge, J., Gossner, M.M., Müller, J. & Heurich, M. (2022). A biodiversity boost from the Eurasian beaver (*Castor fiber*) in Germany's oldest national park. *Front. Ecol. Evol.* **10**, 873307.

Paladi, V. & Cassir, P. (2022). First report of Eurasian beaver (*Castor fiber* Linnaeus 1758) in the Republic of Moldova. *North West. J. Zool.* **18**, 71–76.

Parker, H. & Rosell, F. (2003). Beaver management in Norway: a model for continental Europe? *Lutra* **46**, 223–234.

Perino, A., Pereira, H.M., Navarro, L.M., Fernández, N., Bullock, J.M., Ceaușu, S., Cortès-Avisanda, A., Van Klink, R., Kuemmerle, T., Lomba, A., Pe'er, G., Plieninger, T., Rey Benayas, J.M., Sandom, C.J., Svenning, J.C. & Wheeler, H.C. (2019). Rewilding complex ecosystems. *Science* **364**, eaav5570.

Phillips, S.J., Dudík, M. & Schapire, R.E. (2017). Maxent software for modeling species niches and distributions (Version 3.4.4). Available at: https://biodiversityinformatics.amnh.org/open_source/maxent Accessed on 14 December 2022.

Pinto, B., Santos, M.J. & 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.

Poldini, L., Vidali, M., Castello, M. & Sburlino, G. (2020). A novel insight into the remnants of hygrophilous forests and scrubs of the Po Plain biogeographical transition area (Northern Italy). *Plant Sociol.* **57**, 17–69.

Pontarini, R., Lapini, L. & Molinari, P. (2019). A beaver from north-eastern Italy (*Castor fiber*: Castoridae, Rodentia). *Gortania* **40**, 115–118.

Pucci, C., Senserini, D., Mazza, G. & Mori, E. (2021). Reappearance of the Eurasian beaver *Castor fiber* L. in Tuscany (Central Italy): the success of unauthorised releases? *Hystrix* **32**, 182–185.

Puttock, A., Graham, H.A., Ashe, J., Luscombe, D.J. & Brazier, R.E. (2021). Beaver dams attenuate flow: a multi-site study. *Hydrol. Process.* **35**, e14017.

Puttock, A., Graham, H.A., Cunliffe, A.M., Elliott, M. & Brazier, R.E. (2017). Eurasian beaver activity water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands. *Sci. Total Environ.* **576**, 430–433.

Queiroz, C., Beilin, R., Folke, C. & Lindborg, R. (2014). Farmland abandonment: threat or opportunity for biodiversity conservation? A global review. *Front. Ecol. Environ.* **12**, 288–296.

Radosavljevic, A. & Anderson, R.P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. *J. Biogeogr.* **41**, 629–643.

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, D.W., Wallach, A.D. & Wirsing, A.J. (2014). Status and ecological effects of the world's largest carnivores. *Science* **343**, 1241484.

Roberts, D.R., Bahn, V., Ciuti, S., Boyce, M.S., Elith, J., Guillera-Arroita, G., Hauenstein, S., Lahoz-Monfort, J.J., Schröder, B., Thuiller, W., Warton, D.I., Wintle, B.A., Hartig, F. & Dormann, C.F. (2017). Cross-validation strategies for data with temporal, spatial, hierarchical, or phylogenetic structure. *Ecography* **40**, 913–929.

Ronnquist, A.L. & Westbrook, C.J. (2021). Beaver dams: how structure, flow state, and landscape setting regulate water storage and release. *Sci. Total Environ.* **785**, 147333.

Rosell, F., Bozser, 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.

Salari, L., Masseti, M. & Silvestri, L. (2020). Late Pleistocene and Holocene distribution history of the Eurasian beaver in Italy. *Mammalia* **84**, 259–277.

Sensi, M., Mazza, G., Mori, E. & Esattore, B. (2020). Valutazione ambientale del fiume Merse associata a campionamenti del granchio di fiume *Potamon fluviatile*. *Atti Soc. Toscana Sci. Nat. Mem. B.* **127**, 121–126.

Serva, D., Biondi, M. & Iannella, M. (2023). The Eurasian beaver range expansion reveals uneven future trends and possible conservation issues: an European assessment. *Biodivers. Conserv.* **32**, 1999–2016.

Shah, V.B. & McRae, B.H. (2008). Circuitscape: a tool for landscape ecology. In *Proceedings of the 7th Python in Science conference (SciPy 2008)*: 62–65. Varoquaux, G., Vaught, T. & Millman, J. (Eds). Pasadena, California.

Siemer, W.F., Jonker, S.A., Decker, D.J. & Organ, J.F. (2013). Toward an understanding of beaver management as human and beaver densities increase. *Hum. Wildl. Interact.* **7**, 114–131.

Slezák, M., Douda, J., Šibíková, M., Jarolímek, I., Senko, D. & Hrivnák, R. (2022). Topographic indices predict the diversity of Red List and non-native plant species in human-altered riparian ecosystems. *Ecol. Indic.* **139**, 108949.

Smeraldo, S., Di Febbraro, M., Ćirović, D., Bosso, L., Trbojević, I. & Russo, D. (2017). Species distribution models as a tool to predict range expansion after reintroduction: a case study on Eurasian beavers (*Castor fiber*). *J. Nat. Conserv.* **37**, 12–20.

Stoch, F. & Genovesi, P. (2016). Manuali per il monitoraggio di specie e habitat di interesse comunitario (Direttiva 92/43/CEE) in Italia: specie animali. ISPRA, Serie Manuali e Linee Guida, 141/2016.

Sutanto, S.J., Vitolo, C., Di Napoli, C., D'Andrea, M. & Van Lanen, H.A. (2020). Heatwaves, droughts, and fires: exploring compound and cascading dry hazards at the pan-European scale. *Environ. Int.* **134**, 105276.

Swinnen, K.R., Strubbe, D., Matthysen, E. & Leirs, H. (2017). Reintroduced Eurasian beavers (*Castor fiber*): colonization and range expansion across human-dominated landscapes. *Biodivers. Conserv.* **26**, 1863–1876.

Tattoni, C., Grilli, G. & Ciolli, M. (2017). Advertising value of the brown bear in the Italian Alps. *Ursus* **27**, 110–121.

Thulin, C.G. & Röcklinsberg, H. (2020). Ethical considerations for wildlife reintroductions and rewilding. *Front. Vet. Sci.* **7**, 163.

Treves, A., Bottero, M., Caprioli, C. & Comino, E. (2020). The reintroduction of *Castor fiber* in Piedmont (Italy): an integrated SWOT-spatial multicriteria based approach for the analysis of suitability scenarios. *Ecol. Indic.* **118**, 106748.

Treves, A., Terenziani, A., Angst, C. & Comino, E. (2022). Predicting habitat suitability for *Castor fiber* reintroduction: MaxEnt vs SWOT-spatial multicriteria approach. *Ecol. Inform.* **72**, 101895.

Tuanmu, M.N. & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Glob. Ecol. Biogeogr.* **23**, 1031–1045.

Valavi, R., Elith, J., Lahoz-Monfort, J.J. & Guillera-Arroita, G. (2023). Flexible species distribution modelling methods perform well on spatially separated testing data. *Glob. Ecol. Biogeogr.* **32**, 369–383.

Vanstaen, L. (2019). Reassessment of the prediction model for the spread of the Eurasian beaver (*Castor fiber* L.) in Flanders. Thesis Dissertation, University of Antwerp, Antwerp, Belgium.

Veloz, S.D. (2009). Spatially autocorrelated sampling falsely inflates measures of accuracy for presence-only niche models. *J. Biogeogr.* **36**, 2290–2299.

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

Viviano, A., Mazza, G., Di Lorenzo, T. & Mori, E. (2022). Housed in a lodge: occurrence of animal species within Eurasian beaver constructions in Central Italy. *Eur. J. Wildl. Res.* **68**, 75.

Warren, D.L. & Seifert, S.N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecol. Appl.* **21**, 335–342.

Wojton, A. & Kukuła, K. (2021). Transformation of benthic communities in forest lowland streams colonised by Eurasian beaver *Castor fiber* (L.). *Int. Rev. Hydrobiol.* **106**, 131–143.

Wróbel, M. (2020). Population of Eurasian beaver (*Castor fiber*) in Europe. *Glob. Ecol. Conserv.* **23**, e01046.

Young, K.R. (2014). Biogeography of the Anthropocene: novel species assemblages. *Prog. Phys. Geogr.* **38**, 664–673.

Zavyalov, N.A., Artaev, O.N., Potapov, S.K. & Petrosyan, V.G. (2015). Beavers (*Castor fiber*) of the Mordovia Nature Reserve: population development history, current state, and prospects. *Russ. J. Biol. Invasions* **6**, 148–164.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Alternative sets of variables used for modeling environmental suitability.

Table S2. Pairwise correlation coefficients among environmental variables.

Figure S1. Background points selected for the modeling of environmental suitability with Maxent.

Figure S2. Effect of variables on environmental suitability for the Eurasian beaver.