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Research Article

Crossing borders: Connectivity analyses reveal potential patterns of range expansion of the Northern raccoon in Europe

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Abstract

Identifying suitable areas and potential expansion corridors for alien species that can pose negative environmental and socio-economic impacts is essential to guide prevention, monitoring, and management activities. The Northern raccoon *Procyon lotor* is an alien species that significantly impacts EU biodiversity and society. This species is currently widespread in most of Central Europe, with increasing populations in southern and eastern countries. In this study, we developed species distribution models to identify areas with the highest suitability for the raccoon in Europe. Then, we employed connectivity modeling to assess potential ecological corridors across Europe. Species distribution models confirmed the broad ecological preferences of the species, predicting large areas of Europe to be suitable for raccoons. Connectivity models showed a generally high connectivity in central and western Europe and highlighted mountain ranges and intensive agricultural areas and/or areas with low annual precipitation levels as the main barriers to dispersal. We identified five potential corridors connecting Central European raccoon populations to Southern Europe. Our results can be useful to identify areas that may be prioritized to allocate monitoring and containment efforts, in order to constrain further raccoon expansion across Europe.

Key words: Climatic suitability, connectivity models, dispersal barrier, invasive alien species, northern Italy, *Procyon lotor*, species distribution models

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Introduction

To contain the negative impacts of invasive alien species on ecosystems and biodiversity, it is crucial to identify suitable areas for their establishment and spread. Mapping these suitable areas will enable informed decisions regarding the allocation of resources towards prevention, monitoring, and management activities (Rodríguez-Rey et al. 2019; Srivastava et al. 2019; Pereira et al. 2023; Biancolini et al. 2024; Viviano et al. 2024). The EU Regulation 1143/2014 provides a list of invasive alien species which pose a significant threat to the EU environment, health, or economy (European Union 2014; Carboneras et al. 2017; Bertolino et al. 2020). Thorough knowledge of the distribution and potential spread within Europe for

these species is particularly important to prioritize risk assessments, predict future spread and thus enable proactive management measures and improved prevention strategies (Bertolino et al. 2020; El-Barougy et al. 2021).

Amongst invasive species of EU concern, the Northern raccoon *Procyon lotor* (hereafter, raccoon) is currently widespread in most of central Europe, with novel populations also established in Southern and Eastern countries (García et al. 2012, Salgado 2018; Boscherini et al. 2019; Valdez et al. 2022; Stope 2023). The high adaptability and opportunistic feeding habits enable the raccoon to thrive in several habitat types, ranging from urban areas to rural landscapes, making it a successful invader (Bartoszewicz et al. 2008; Salgado 2018; Zeveloff 2024). Furthermore, multiple introductions have overcome the potential bottlenecks, thus increasing the genetic variability which may have helped the raccoon spread in Europe (Fischer et al. 2017; Garofalo et al. 2024). Raccoons are known to outcompete native species for food and shelter (Kauhala 1996; Salgado 2018; Ważna et al. 2024) and to prey on them, often leading to population declines (e.g., native crayfish *Austropotamobius pallipes* complex in Italy: Boncompagni et al. 2021; Tricarico et al. 2021; hibernating bats in Poland: Cichocki et al. 2021). Moreover, raccoons can transmit diseases to both humans and native wildlife, posing a significant health risk (Beltrán-Beck et al. 2012; Lombardo et al. 2022; Maas et al. 2022). All these impacts highlight the importance of monitoring existing invasive raccoon populations and preventing their further expansion (Nentwig et al. 2018; Mazzamuto et al. 2020; Kochmann et al. 2021). The high ecological plasticity of the raccoon may imply that high portions of suitable habitats are not yet occupied throughout Europe, also given that climatic conditions do not appear to restrict its range expansion (Fischer et al. 2016; Louppe et al. 2019; Kochmann et al. 2021). Predicting potential distribution and understanding the preferential areas through which raccoon populations may expand across Europe can provide valuable insights for forecasting future range shifts. This, in turn, will inform wildlife managers about potential hotspots for deploying targeted removal strategies (Fischer et al. 2016; Salgado 2018; Boscherini et al. 2019; Kalandarishvili and Heltai 2019; Mazzamuto et al. 2020).

Previous studies already used species distribution models to identify potentially suitable areas for the raccoon at the global scale (Louppe et al. 2019; Kochmann et al. 2021; Cunze et al. 2023). Still, the non-equilibrium of species distribution in the invaded range was often overlooked, possibly leading to overfitting (i.e., the excessive dependence of model parameters on environmental conditions found in the calibration area). The issue of overfitting is particularly relevant for invasives because the aim is usually to predict suitable areas outside the known distribution of the target species (Elith et al. 2010; Mainali et al. 2015; Fourcade 2021). This means that it is crucial to find a balance between model flexibility, which is needed to capture complex species-environment relationships, and overfitting, which should be minimized to avoid modeling the spatial structure of the training points, allowing the production of meaningful predictions outside the geographic space of model training (Moreno-Amat et al. 2015; Valavi et al. 2023).

In this study, we developed species distribution models to identify areas with the highest raccoon suitability in Europe. Furthermore, we employed connectivity modeling to assess potential dispersal routes across Europe, in order to assist environmental managers in prioritizing areas to monitor and perform containment measures.

Methods

Distribution and environmental data

This study focuses on the invasion of the raccoon in Europe, therefore we considered two main areas: Europe, west to the Ural Mountains and Black Sea, and Central and North America, as the invaded and native ranges of the raccoon, respectively. Recent raccoon occurrence records (collected after 1980) in both native and alien ranges were retrieved from the Global Biodiversity Information Facility (GBIF; https://www.gbif.org/; https://doi.org/10.15468/dl.j32az3) and from iNaturalist (https://www.inaturalist.org/) on 1st October 2023. We kept only "research grade" records from iNaturalist (i.e., identification confirmed by the community), while GBIF records were filtered by: *i*) selecting only records marked as "PRESENT" under the column "occurrenceStatus", and *ii*) removing records with identical latitude and longitude since they are likely to be copy-paste errors. For both databases, only records with coordinate precision <500 m were kept. These records were integrated with 68 records from northern and central Italy, which are areas reported to be hotspots of alien animal biodiversity (https://specieinvasive.isprambiente.it/documenti-utili/rendicontazione; Accessed on 03.04.2025). These records were retrieved by the authors through direct observation, camera trapping, gray literature, or social networks (Suppl. material 1). Occurrence records were projected to the Mollweide reference system (EPSG: 54009), which is an equal area projection appropriate for global analyses. Occurrences from North America but very far (>200 km) from the native range provided by the IUCN (Timm et al. 2016) were discarded. Finally, redundant records were removed by keeping only one record within 1×1 km cells, obtaining a total of 38,068 records: 32,834 for North America and 5,234 for Europe. To limit the potential bias arising from an unbalanced sampling effort and to improve model transferability, occurrences from the native range were rarefied (Radosavljevic and Anderson 2014; Aiello-Lammens et al. 2015), removing records in adjacent cells by using a thinning distance of two times the diagonal length of the cells (~2.83 km in our case), using the spThin R package (Aiello-Lammens et al. 2015). Therefore, the final dataset included a total of 19,154 records used for training species distribution models.

As potential environmental predictors, we used a combination of climatic, topographic, and land cover variables. The choice of variables was based on the known ecology of the species and was structured in order to include alternative climatic predictors relating to temperature, temperature variation, precipitation, and precipitation variation (Louppe et al. 2019; Kochmann et al. 2021; Grüneberger 2022, Gautrelet et al. 2024). These variables included: mean annual temperature (Bio1), mean diurnal temperature range (Bio2), mean daily maximum temperature of the warmest month (Bio5), mean daily minimum temperature of the coldest month (Bio6), mean temperature of the warmest quarter (Bio10), annual precipitation amount (Bio12), precipitation seasonality (Bio15), mean monthly precipitation amount of the driest quarter (Bio17), mean monthly precipitation amount of the warmest quarter (Bio18), slope, agricultural cover, forest cover, and snow/ice cover. Climatic variables were retrieved from CHELSA 2.1, relating to the 1980-2010 climatologies (Karger et al. 2017). The slope was calculated using the "terrain" function from the raster R package (Hijmans 2023), starting from the elevation map at 30 arc-second resolution retrieved from the WorldClim dataset, version 2.1 (Fick and Hijmans 2017). Land cover variables were retrieved from

the EarthEnv dataset (Tuanmu and Jetz 2014). All maps were projected to the Mollweide coordinate reference system at a resolution of 1×1 km. Environmental predictors were not used all together in a single model, but we prepared 40 alternative variable sets, including different combinations of bioclimatic, topographic, and land cover variables. In each set, we avoided the inclusion of variables showing Pearson correlation coefficients >|0.7| (Suppl. material 2: fig. S2.1, table S2.1). These variable sets, along with different model complexities, were tested with the procedure shown below.

Species distribution models

We modeled environmental suitability using Maxent (Phillips et al. 2017), version 3.4.3. While Maxent is among the best-performing algorithms to predict suitability outside calibration areas, machine learning algorithms are often prone to overfitting issues (Valavi et al. 2023). This means that when predicting suitability outside of the calibration area, the results obtained can be unreliable when overfitting is strong (Ludwig et al. 2023). To assess the potential distribution of a species outside its native range, it is therefore essential to limit overfitting while allowing some flexibility in environment-suitability relationships (Valavi et al. 2023). Hence, we adopted a workflow aimed at minimizing overfitting and maximizing the transferability of the model outside the calibration area (i.e., the native range of the species, given that raccoon distribution is not at equilibrium in Europe).

Given that sampling bias is one of the main issues of citizen science data (Hughes et al. 2021), we sampled background points by maintaining the same bias shown by occurrence records. This was achieved by calculating the kernel density of occurrences and then assigning to each cell of the raster a value between 0 and 1, based on rescaled values of the kernel (Kass et al. 2022). Then, we sampled 40,000 unique backgrounds using these values as the probability for each cell to be sampled. Kernel density was calculated using the "sp.kde" function from the spatialEco R package (Evans and Murphy 2023).

As shown by Fourcade et al. (2018), classic metrics of model evaluation based on random splitting of training and testing data can strongly overestimate model performance, being unrelated to model spatial transferability. Dividing the study area into a few (spatially separated) blocks enable testing the true transferability of species distribution models. Therefore, similarly to Falaschi et al. (2024), we used spatially separated testing data to ensure transferable predictions (Radosavljevic and Anderson 2014). Then, we split both occurrences and backgrounds into four blocks using the "get.block" function from the ENMeval R package (Kass et al. 2021). Groups were created by splitting the points first by latitude and second by longitude, in order to obtain a balanced number of both occurrences and backgrounds within each group. Then, the four groups were merged into two groups used for spatially separated cross-validation: one group included northeastern and southwestern points (NE-SW), and the other included northwestern and southeastern points (NW-SE). In this way, we obtained a balanced partitioning into 9,577 occurrences and 19,083 backgrounds for the NE-SW group, and 9,577 occurrences and 20,917 backgrounds for the NW-SE group, as shown in Fig. 1.

To allow some flexibility of species-environment relationships, we tested two combinations of Maxent features (linear + quadratic, linear + quadratic + hinge) and ten values of the regularization multiplier (from 1 to 10), which is a parameter regulating

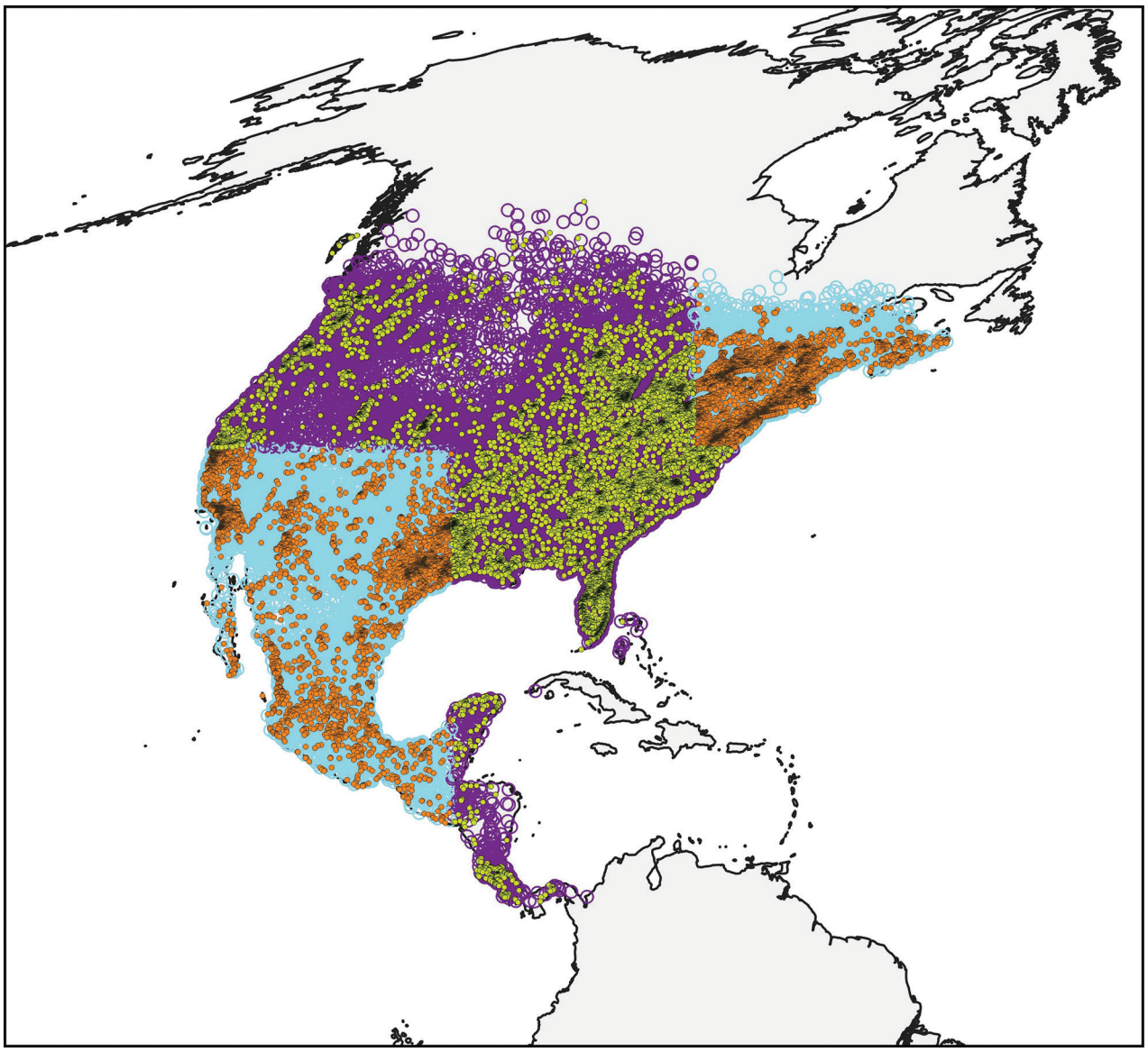

Figure 1. Spatially separated partitions of occurrence and background data from the raccoon's native range. Open violet and azure dots represent 40,000 backgrounds, and closed green and orange dots represent the 19,154 occurrences used for the training of Maxent models.

the complexity of variable-suitability relationships (Merow et al. 2013). Therefore, we had a total of 800 combinations: 40 variable sets × 2 feature combinations × 10 regularization multiplier values. The standardized protocol for reporting species distribution modeling development (Zurell et al. 2020) is available in Suppl. material 3.

Selection of the best species distribution model

For each combination of variable set, feature, and regularization multiplier, we ran Maxent twice: one with NE-SW and one with NW-SE partition. Each model run was projected on the opposite partition, in order to calculate four statistics: two measures of model performance, the Area Under the receiver operating characteristic Curve (AUC), and the Continuous Boyce Index (CBI; Hirzel et al. 2006), and two measures of model overfitting, here named AUC overfitting and CBI overfitting. Overfitting measures were calculated as the difference between AUC or CBI on training data and AUC or CBI on testing data (Radosavljevic and

Anderson 2014), therefore low values represent models that perform similarly in both training and testing areas. AUC and CBI were calculated using the ROCR (Sing et al. 2005) and ecospat (Di Cola et al. 2017) R packages.

To select the model that maximized the performance while minimizing overfitting, we ran a principal components analysis on the average AUC, CBI, AUC overfitting, and CBI overfitting of the two spatial replicates of each combination of variables, features, and regularization multipliers. Then, we identified the best combination of variables, features, and regularization multiplier as the one with high values of AUC and CBI and low values of overfitting. Principal components analysis was run using the vegan R package (Oksanen et al. 2024). Finally, the best combination of variables, features, and regularization multiplier was used to run a model (best model) trained on all occurrences and backgrounds of the two partitions (19,154 occurrences and 40,000 backgrounds). The best model was used to obtain suitability for Europe for subsequent connectivity analyses. All the Maxent models were run using the dismo R package (Hijmans et al. 2023). To test potential niche truncation of projecting a model trained on native range data to Europe, we performed a multivariate environmental similarity surfaces analysis, using the "mess" function from the dismo R package (Hijmans et al. 2023), in order to highlight areas outside the range of calibration. Additionally, we performed a comparison of the environmental niche in the native and invasive ranges, to check for potential niche expansion (Suppl. material 4).

Data preparation and analyses were performed in R, version 4.3.2 (R Core Team 2023). A script showing the modeling procedure is available at Figshare: https://doi.org/10.6084/m9.figshare.27311484.v1.

Connectivity modeling

To identify possible expansion trajectories of raccoons across uninvaded areas of Europe, we modeled environmental connectivity through an omni-directional connectivity approach, using the Omniscape software (Landau et al. 2021; Liczner et al. 2024). The Omniscape algorithm applies Circuitscape (Shah and McRae 2008) iteratively across the landscape in the "advanced" mode. A moving window with a radius specified by the user is used to mask the landscape around each possible source cell. Then, the current flow between this cell and all the other possible source pixels within the moving window is calculated. Finally, the current flow is summed across all the moving windows to obtain a map of the cumulative current (Landau et al. 2021).

The map of resistance was obtained by modifying the suitability map of Maxent with the following procedure. Previous works demonstrated that the best approximation to derive landscape resistance from suitability maps is a negative exponential transformation with a steep decrease in resistance at increasing values of suitability (Keeley et al. 2016; Wright et al. 2021). Here, suitability was transformed into resistance by applying a reciprocal transformation (resistance = 1/suitability), which closely reflects the transformations used in previous works (Suppl. material 2: fig. S2.2) without the need to specify any additional parameter. Then, given that large water bodies, mountains, and large infrastructure can be barriers to the spread of raccoons (Wheeler and Waller 2008; Côté et al. 2012; Červinka et al. 2015; Gautrelet et al. 2024), cells mainly covered (>75%) by large water bodies (i.e., the ones mapped at the 1-km resolution of

Tuanmu and Jetz 2014), built-up, or snow and ice, were set to high resistance (100 ohms, i.e., a very high value almost preventing current flow). Water, built-up, and snow/ice cover were retrieved from the EarthEnv dataset (Tuanmu and Jetz 2014). We ran Omniscape from Julia, setting all non-NA raster cells as potential sources ("source_from_resistance = true"). The search radius was set at 50 cells (i.e., 50 km, which is close to the known maximum dispersal distance of raccoons; Hohmann and Bartussek 2001). To reduce computation times, we set "block size" to five (1/10 of the search radius), hence selecting one every 25 cells as possible current source (Phillips et al. 2021). An alternative approach could be the use of known occurrence localities as sources, and the borders of the study area as grounds (i.e., running Circuitscape in "advanced" mode, once for each occurrence record; e.g., Cowley et al. 2015; Falaschi et al. 2018; Giuntini et al. 2022). Still, the results can change based on several factors, including sampling bias in the invaded range, spatial thinning of occurrences, and values of the resistance layer at current input locations. All these sources of variation should be standardized by the Omniscape approach used in this work.

Results

Selection of the best species distribution model

Maxent models tested on spatially separated data showed large variations in both performance and overfitting measures (Suppl. material 2: table S2.2). AUC test and CBI test values, averaged between the two replicates, ranged respectively between 0.490–0.669 and -0.168–0.999. AUC overfitting and CBI overfitting values, averaged between the two replicates, ranged respectively between -0.009–0.102 and -0.197–0.863.

The first axis of the principal components analysis used to identify the best model explained more than 60% of the variance, with lower values of this component corresponding to high values of AUC test and CBI test and low values of CBI overfitting (Fig. 2). The second principal component explained 25% of the variance and was mainly related to AUC overfitting, with high values of this component corresponding to lower AUC overfitting. Therefore, we selected the best model as the one showing low values of the first principal component and high values of the second principal component. This model included: *i*) five variables: mean annual temperature (Bio1), annual precipitation amount (Bio12), slope, agricultural cover, and forest cover; *ii*) linear, quadratic, and hinge features; *iii*) a regularization multiplier of 2. This model showed a positive relationship between both Bio1 and Bio12 and suitability, suggesting the highest suitability in areas with mean annual temperatures above 0 °C and with more than 1,000 mm/year of precipitation (Suppl. material 2: fig. S2.3). Suitability decreased at high levels of slope, agricultural cover, and forest cover (Suppl. material 2: fig. S2.3).

Habitat suitability and connectivity across Europe

The suitability model suggested very high suitability across many areas of the European continent, particularly in central and western Europe, in southern Scandinavia, and in the United Kingdom and Ireland (Fig. 3). Areas with low suitability included the coldest regions such as Scandinavia, Russia, the Alps,

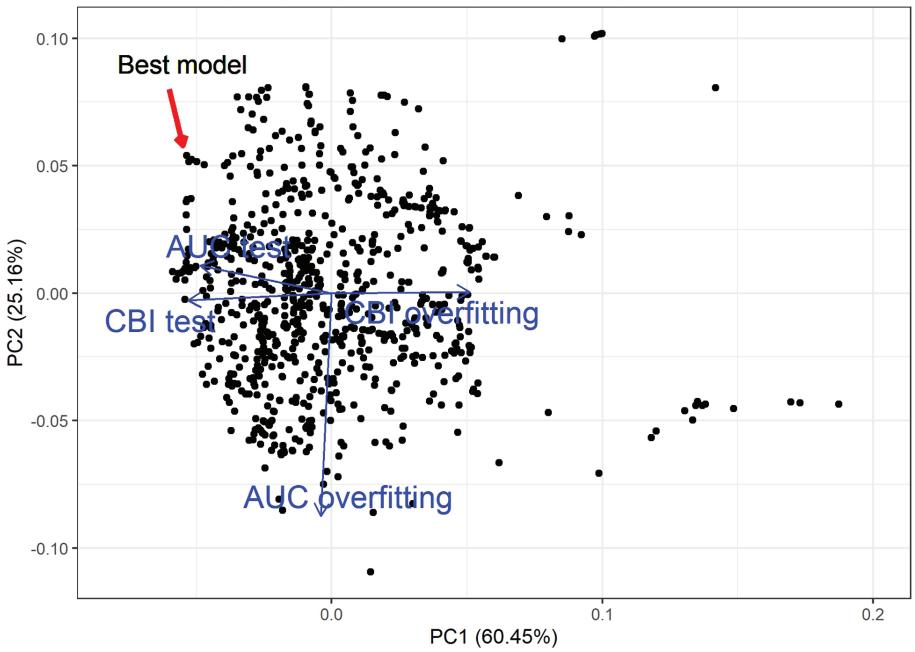

Figure 2. Principal component analysis based on performance (AUC test and CBI test) and overfitting (AUC overfitting and CBI overfitting) values of the 1,600 Maxent models tested on spatially separated data (800 combinations of variables, features, and regularization multiplier ×2 partitions). The red arrow indicates the best model, chosen as the model showing a low value of the first principal component (PC1; corresponding to high values of AUC test and CBI test and low values of CBI overfitting) and high values of the second principal component (PC2; corresponding to low values of AUC overfitting).

and the Pyrenees, and intensive agricultural areas and/or areas with low annual precipitation amounts such as northern Spain, eastern United Kingdom, western France, southern Italy, and eastern Europe (Fig. 3). The extrapolation analysis showed that only very small areas in the Alps were outside the model calibration range (Fig. 3b), indicating the absence of niche truncation issues. The niche analysis showed the complete absence of niche expansion (Suppl. material 4), indicating that environmental conditions exploited by raccoons in Europe were a subset of the ones exploited in the native range.

Areas with high resistance mirrored the lowest suitable areas, also including large water bodies, large urban centers, and areas permanently covered by ice or snow (Fig. 4). The connectivity model highlighted high current flow in central and western Europe, and generally a lower current flow in eastern Europe. North-western France and the Alps were highlighted as the main barriers around the main area invaded by raccoons in central Europe (Fig. 5a). When focusing on the connectivity between the two main hotspots of invasion (i.e., central Europe and central Italy), potential corridors for raccoon diffusion were highlighted in both western and eastern areas of the Alpine arc, even if connectivity showed generally low values (Fig. 5b). In the western portion, the highest connectivity was found along the coast of the Tyrrhenian Sea and along the Susa Valley, connecting France to western Piedmont region (Italy). In the eastern portion, two clear corridors were identified: the Vinschgau Valley and the Eisack Valley, both connecting southwestern Austria to Trentino-Alto Adige region (Italy). Additionally, high current flow was highlighted also eastward to the Alpine arc, potentially allowing the colonization of northeastern areas of Italy from Austria or Slovenia (Fig. 5b).

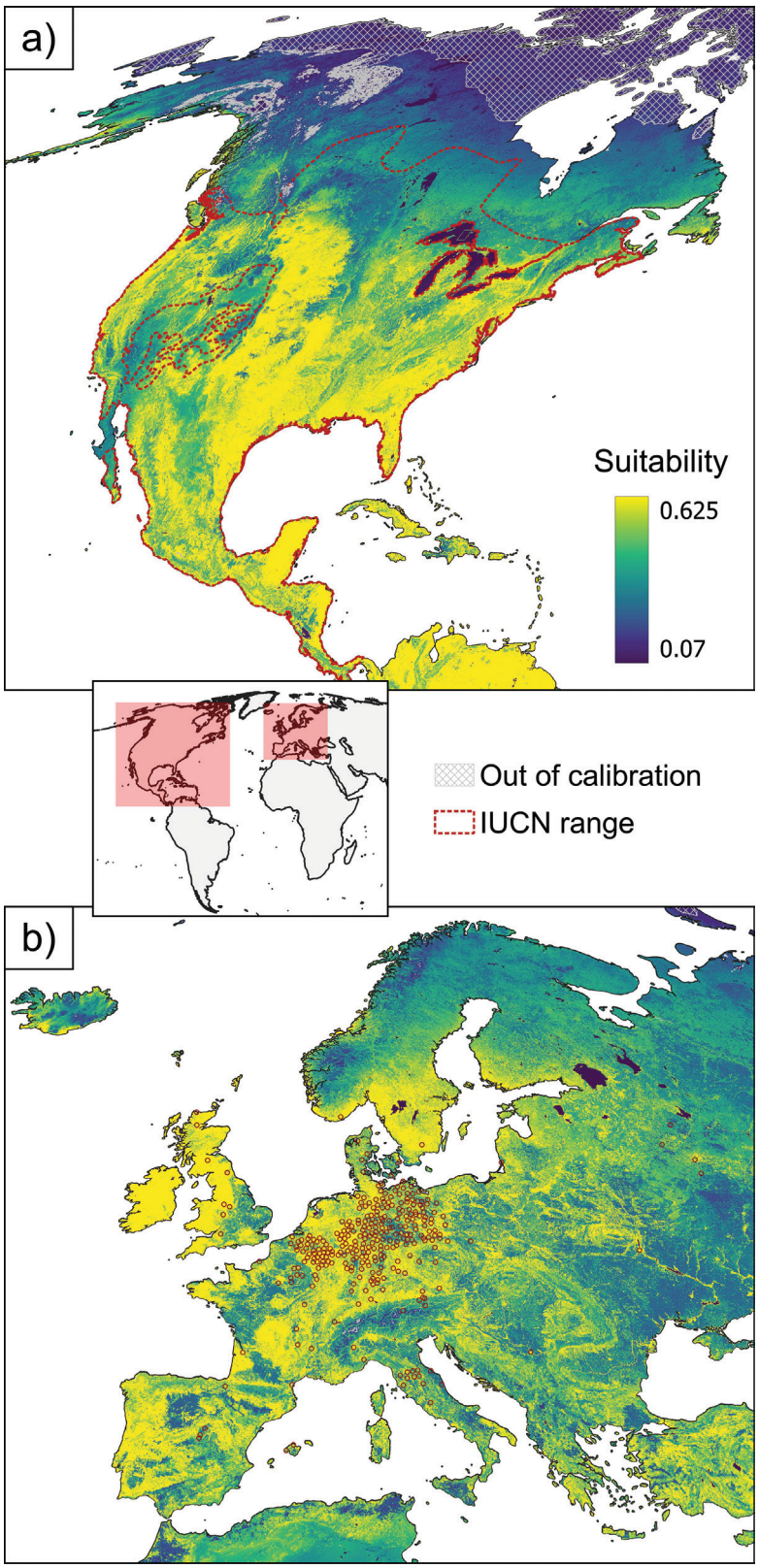

Figure 3. Climatic suitability for the raccoon, predicted by the best Maxent model based on spatially separated training and testing data, for the native range (**a**) and Europe (**b**). The red dotted line in **a** represents the IUCN range of the species. Raccoon occurrences in Europe are shown as red dots in **b**, where only one observation each 25 km is shown for better visualization. The suitability thresholds correspond to the minimum training presence (0.07) and the maximum training sensitivity plus specificity (0.625). Areas outside the calibration range are shown with a gray lines overlay (in Europe these areas are limited to small spots on the Alps and in northern Scandinavia). The map (in GeoTIFF format) is available at Figshare: https://doi.org/10.6084/m9.figshare.27311484.v1.

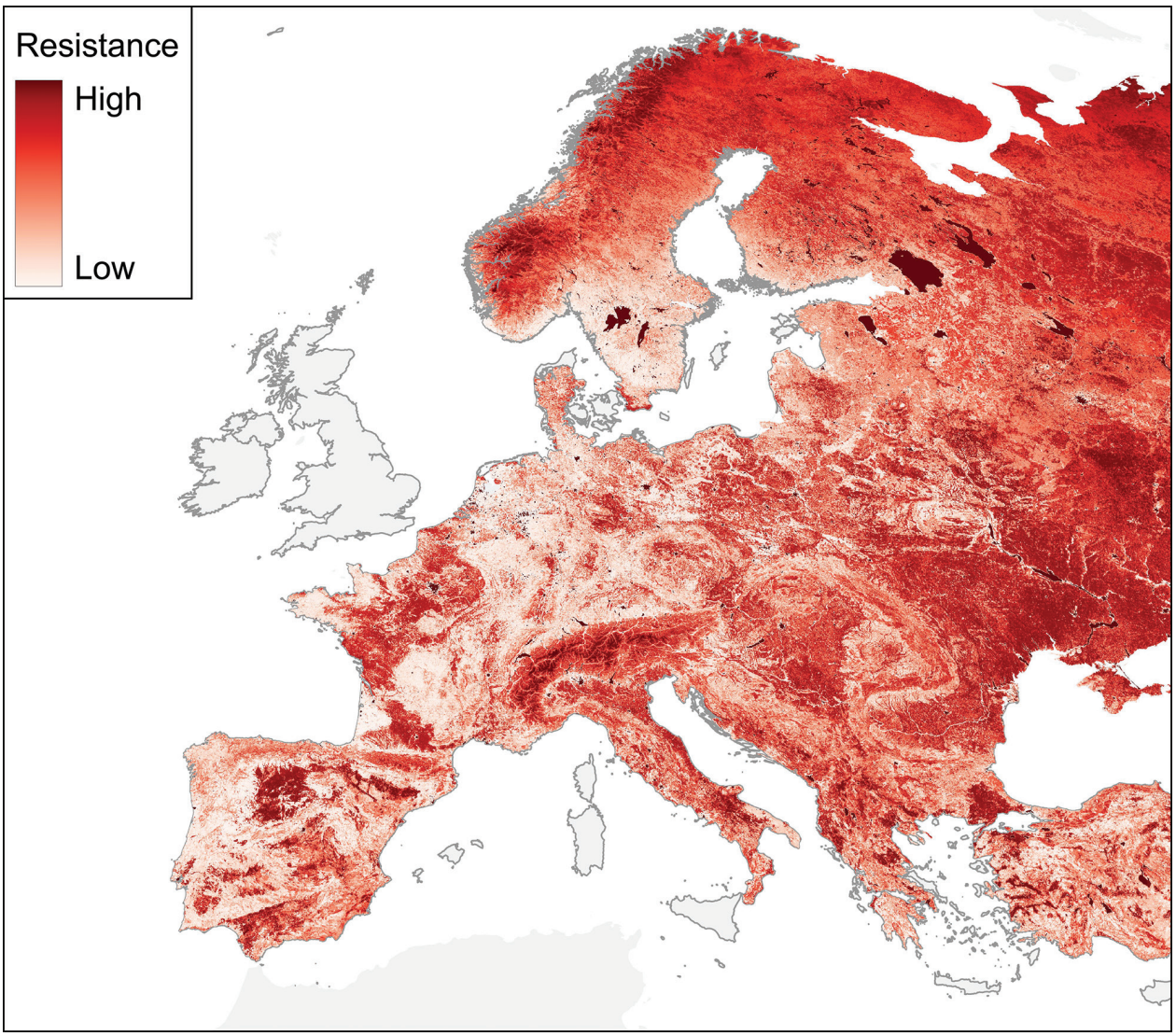

Figure 4. Resistance map used as a base for connectivity modeling. White areas represent cells with low resistance and dark red areas are cells with high resistance (range 0–100). Only mainland Europe was considered and islands were excluded from the connectivity analysis. The map (in GeoTIFF format) is available at Figshare: https://doi.org/10.6084/m9.figshare.27311484.v1.

Discussion

In this study, we identified large areas of Europe that are suitable for raccoons and not yet invaded. Connectivity at the European level was generally high, with barriers being the main mountain chains and intensive agricultural areas and/or areas with low annual precipitation. Given the high connectivity and the broad availability of uninvaded suitable areas, special attention is required to prevent further spread of this invasive species.

While species distribution models are widely used to predict the potential distribution of alien species in space and time (Louppe et al. 2019; Ramellini et al. 2019; Mori et al. 2021), several issues can hamper the transferability of these models (Liu et al. 2020). Among others, sampling bias and non-equilibrium of species distributions with the environment can increase overfitting and decrease the predictive power of models outside the area of calibration (Kramer-Schadt et al. 2013; Fourcade 2021; Freeman et al. 2022). Additionally, spatial autocorrelation may lead to the inclusion of predictors that are not relevant to the ecology of the species, hence hampering the identification of the true niche of the species (Veloz 2009; Fourcade

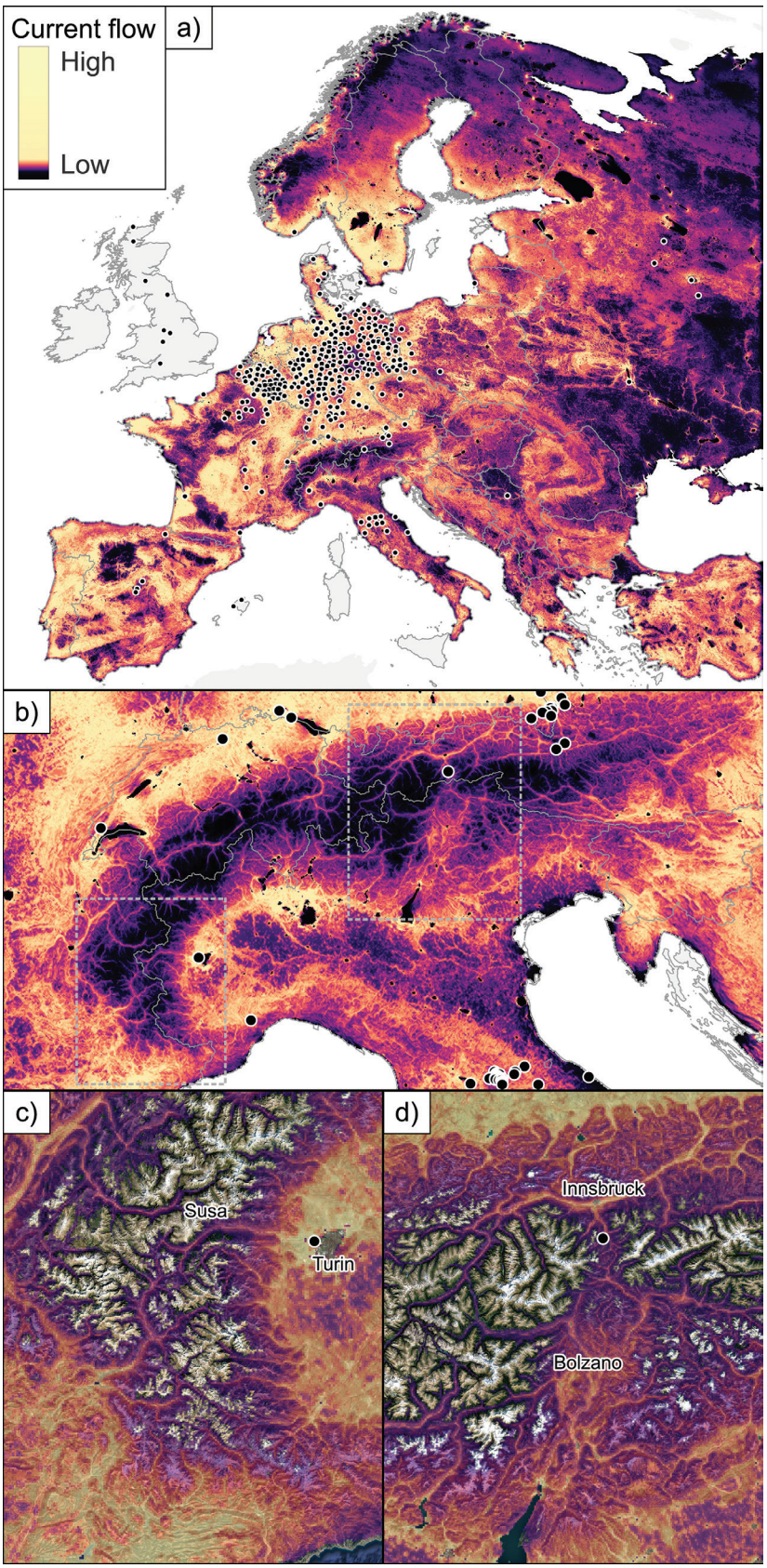

Figure 5. Current flow estimated by the Omniscape analysis across Europe (**a**) and in the Alps region (**b**). Potential corridors through the Alpine arc are highlighted with dashed lines in **b** and shown in **c** and **d**. In all the panels, raccoon occurrences are shown as black dots, and in **a** only one observation each 25 km is shown for better visualization. Satellite imagery in **c** and **d**: ©2024 TerraMetrics, accessed through Google Maps. The map (in GeoTIFF format) is available at Figshare: https://doi.org/10.6084/m9.figshare.27311484.v1.

et al. 2018). Here, we adopted several measures to minimize these issues. First, background points were sampled with the same spatial bias of occurrences to correct for sampling bias (Phillips et al. 2009; Kass et al. 2022). Second, we trained the model using data exclusively from the native range, given that the inclusion of areas where the species distribution is not at equilibrium (i.e., Europe for the raccoon) will likely lead to overfitted models, possibly underestimating species potential distribution (Freeman et al. 2022). Finally, to decrease overfitting due to spatial autocorrelation, we divided data into two spatially separated partitions, allowing us to test the performance of alternative models on truly independent data (Radosavljevic and Anderson 2014; Fourcade et al. 2018). This strategy should avoid the inclusion of predictors not relevant to the ecology of the species while allowing for flexibility in the models (Radosavljevic and Anderson 2014; Fourcade et al. 2018; Valavi et al. 2023). Compared to currently available models assessing the potential distribution of raccoons in Europe (Louppe et al. 2019; Kochmann et al. 2021; Cunze et al. 2023), our results more closely align with Louppe et al. (2019) which adopted strategies to minimize spatial autocorrelation and overfitting issues, such as occurrences filtration. Being focused on changes in suitability due to future climatic conditions, their model did not include land cover or topographic predictors. Hence, our model captures variation in suitability at a much finer scale (Fig. 3), and the main differences compared to Louppe et al. (2019) included a lower suitability of our model in some areas of central and western France and a higher suitability in south-western Iberian peninsula, while in both models suitability generally declined moving to eastern Europe.

The connectivity map showed a generally high connectivity across Europe (Fig. 5a). On the one side, the main invasion cluster in central Europe is surrounded by two areas with lower connectivity: i) northern France, and ii) central Poland and Czech Republic. On the other side, central and southern France seem to be highly connected with the central European cluster, suggesting that focusing monitoring and control measures on the southwestern side of the invasion front of central Europe may be crucial to avoid further expansion in large uninvaded areas. Looking at less invaded areas, the southern Scandinavia peninsula showed both high suitability and connectivity and only a few raccoon records (Figs 3, 5). Habitat was predicted to be particularly suitable in large areas of southern Sweden (Fig. 3), therefore, even if this area is not directly connected to the main invasion hotspot of central Europe, human-mediated dispersal events are always possible (Mosillo et al. 1999; Skírnisson 2022; Garofalo et al. 2024), particularly considering the free circulation of vehicles and goods within Member States of the European Union. A further aspect of raccoon adaptability and expansion is their ability to stow away in containers, trucks, and ships, leading to human-mediated spread beyond their native range or throughout the invasive one (Skírnisson 2022). Human activities have played a significant role in the spread of raccoons beyond their native range. As generalist opportunists, raccoons readily explore cargo containers, vehicles, and shipping vessels in search of food and shelter, sometimes inadvertently traveling great distances (Skírnisson 2022). This phenomenon raises important ecological and management concerns, particularly when considering the distinction between natural range expansion and anthropogenic introduction (Hill et al. 2023). Strict biosecurity protocols are essential to limit this relevant phenomenon.

Unlike central Europe, a different scenario emerged for Italy. Here, thanks to the presence of the Alpine arc and the patchy distribution of raccoon populations, areas of potential expansion of this species are much more restricted (Fig. 5b). Monitoring and containment efforts in northern Italy would foster a prompt and efficient

eradication as the one carried in the Adda river between 2016 and 2019, which successfully eradicated one of the largest raccoon populations in Italy (Mazzamuto et al. 2020). The establishment of new populations in northern Italy would nullify past removal actions, while the contact of disjunct populations may increase their genetic variability, potentially accelerating future expansion. Monitoring and management activities may focus on five main areas: the Susa Valley and Tyrrhenian coast in the west (Fig. 5c) and the Vinschgau Valley, the Eisack Valley, and the Italy-Slovenia border in the east (Fig. 5b, d). However, these efforts should be paired with intensified containment measures in central Italy, where raccoons are already abundant (Fig. 3) and where suitable areas seem to be substantially connected (Figs 3, 4).

Conclusion

The invasion of Europe by the raccoon can pose important ecological threats and societal challenges and intense educational, monitoring, and containment efforts are required to safeguard biodiversity and limit human-wildlife conflicts (Boncompagni et al. 2021; Cichocki et al. 2021; Stope 2023). Our analyses suggested that, while raccoon invasion may proceed unconstrained in certain areas of western Europe, eastern Europe showed generally less connectivity and suitability (Figs 3, 5). Additionally, the arrangement of the Alpine arc facilitates monitoring and containment efforts in northern Italy.

The identified routes through the Alps for raccoon dispersal could potentially be used by other invasive species that are currently established in Europe but have only been sporadically recorded in Italy, such as the raccoon dog *Nyctereutes procyonoides* (Duscher and Nopp-Mayr 2017; Pecorella et al. 2023). Additionally, this corridor may also facilitate the movement of several species of conservation interest at the European level, including the Eurasian beaver *Castor fiber* (Falaschi et al. 2024; Serva et al. 2024), the Eurasian lynx *Lynx lynx* (Molinari-Jobin et al. 2018; Iannella et al. 2024), the golden jackal *Canis aureus* (Torretta et al. 2020; Serva et al. 2023), the European hare *Lepus europaeus* (La Morgia et al. 2023), and the Eurasian otter *Lutra lutra* (Leoncini et al. 2023). Given their potential role in shaping species distributions, these corridors require systematic monitoring to enable early detection of both invasive and native species expanding their range. Implementing targeted conservation and management strategies tailored to each species is essential to mitigate the ecological impact of invasive species while promoting the protection and connectivity of populations of conservation concern. This highlights the need for cross-border collaboration and coordinated efforts in wildlife surveillance, habitat management, and policy development to address the challenges associated with species movements in a rapidly changing landscape. Targeted interventions focused on a limited number of focal areas may thus help to mitigate the expansion of raccoons. Implementing systematic camera trapping monitoring may be a cost-effective tool to assess wildlife exploiting these corridors (Green et al. 2018; Park et al. 2021; Pecorella et al. 2023). Recent developments in automatic species identification from camera trapping images may help in building a system to trigger control interventions when alien species are detected (Norouzzadeh et al. 2018).

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: MF, EM. Data curation: LA, AV, MM, GM, EM. Formal analysis: MF, AS. Methodology: MF, AS. Supervision: EM. Writing – original draft: MF, EM. Writing – review and editing: All authors.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information. Data and scripts used to run suitability models are available at Figshare: https://doi.org/10.6084/m9.figshare.27311484.v1.

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Supplementary material 1

Raccoon distribution in Italy

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Supplementary material 2

Supplementary figures (figs S1–S3) and tables (tables S1, S2)

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Supplementary material 3

ODMAP Protocol

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Supplementary material 4

Niche comparison between North America and Europe

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