




PREDICTIVE REVIEW

Climatic niche comparison of raccoons *Procyon lotor* and raccoon dogs *Nyctereutes procyonoides* in their native and non-native ranges

Judith KOCHMANN*  *Senckenberg Biodiversity and Climate Research Center, Senckenberganlage 25, 60325 Frankfurt am Main, Germany. Email: judith.kochmann@senckenberg.de*

Sarah CUNZE  *Institute of Ecology, Evolution and Diversity, Goethe University, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany. Email: cunze@bio.uni-frankfurt.de*

Sven KLIMPEL  *Senckenberg Biodiversity and Climate Research Center, Senckenberganlage 25, 60325 Frankfurt am Main, Germany and Institute of Ecology, Evolution and Diversity, Goethe University, Max-von-Laue-Str. 13, 60438 Frankfurt am Main, Germany. Email: klimpel@bio.uni-frankfurt.de*

Keywords

Carnivora, ecospat, invasive mammals, Maxent, range expansion

*Correspondence

Received: 30 September 2020

Accepted: 14 December 2020

Editor: DR

doi: 10.1111/mam.12249

ABSTRACT

1. During the last century, the practice of fur farming in Europe led to the introduction of two mammal species from opposite ends of the world. With their subsequent unintentional escape from captivity or intentional releases, the process of slow expansion and establishment in Europe began. The raccoon *Procyon lotor* and the raccoon dog *Nyctereutes procyonoides* are included on the European Union's list of invasive alien species.
2. We characterised the current climatic niches of the two species in their native ranges in North America and Asia, and compared them with their non-native-range niches in Europe, where we also projected climatic suitability. The aim was to locate suitable habitats beyond their current ranges and assess where a range expansion can be expected.
3. Niche comparison and the projection of climatic suitability in Europe were based on eight bioclimatic variables and presence records from the Global Biodiversity Information Facility database. For niche modelling, we applied the maximum entropy approach (Maxent) and used the native-range data for training.
4. Minimum temperature of the coldest month (bio06) was identified as the most important bioclimatic variable in the habitat suitability models for both species. Different tolerance levels regarding this variable might explain small differences between the species' projected ranges, especially in the north and east of Europe. The high niche unfilling for both species in Europe suggests a potential for expansion beyond their present ranges.
5. With only little understanding of their ecological impacts in their new ranges, including the potential risk of *Nyctereutes procyonoides* as SARS-CoV-2 reservoir hosts, further research and management is required at various spatial scales in Europe.

INTRODUCTION

Examples from all around the globe show that mammals have a high potential to become invasive once they have been introduced to an area (Jeschke & Strayer 2005). Population control and eradication efforts have been successful for invasive mammals on islands (Courchamp et

al. 2003, Jones et al. 2016), but finding long-term management options is often challenging (Bertolino et al. 2020, Mill et al. 2020). Perception of invasive alien species as charismatic can also lead to opposition of their control (Jarić et al. 2020). A common approach in invasive species management is to use species distribution models,

which can guide early detection and rapid response measures (Srivastava et al. 2019). Based on past experiences and the potentially devastating outcomes for native flora and fauna, 11 mammal species are now included on the European Union's list of invasive alien species (EU regulation 1143/2014). Member states are required to take action to stop further introductions, implement monitoring, control introduction pathways, and manage already established populations to minimise further spread.

Among the species listed are the raccoon *Procyon lotor* and the raccoon dog *Nyctereutes procyonoides*, both belonging to the order Carnivora. They have been introduced to Europe from opposite sides of the globe, mainly for fur farming and hunting purposes. Whereas populations of *Procyon lotor* have been on the rise annually since 1994 in Central Europe, numbers of *Nyctereutes procyonoides* declined due to a canine distemper outbreak in 2007 and are still much lower than those of *Procyon lotor* (Mulder 2012, Salgado 2018).

Procyon lotor originates from the North American continent and was deliberately introduced into Europe in the early 1920s. The largest non-native populations are found in Germany, from where the species originally started expanding into neighbouring countries (Hohmann & Bartussek 2018). Other non-native populations exist in Japan and the Caucasus. *Nyctereutes procyonoides* is native to East Asia, its distribution ranges from south-eastern Siberia to northern Vietnam and the Japanese islands. It belongs to the family Canidae and is the only extant species of the genus *Nyctereutes*. In the early 20th century, it was introduced into western parts of Russia, from where it slowly expanded into Scandinavia, the Baltic states, and, by the 1960s, Poland and Germany (for further details, see Kauhala & Kowalczyk 2011, Mulder 2012).

Habitat use of the two species can be described as opportunistic, mostly depending on the availability of food and shelter. *Procyon lotor* is found in deciduous and mixed forests where it climbs trees in search of resting hollows, but it also roams in swamps and marshes, and population density can reach >100 individuals per 100 ha in urban environments (Hohmann & Bartussek 2018). Agricultural habitats are also used, but seemingly to a lesser extent than in its native range (Beasley et al. 2007). *Nyctereutes procyonoides* uses various habitats, from coniferous forests and wetlands (Melis et al. 2015, Duscher & Nopp-Mayr 2017) to agricultural landscapes (Drygala et al. 2008). It uses burrows for resting and reproduction (Mulder 2012). Both species have an omnivorous diet, which is influenced by season and locality (Sutor et al. 2010, Engelmann et al. 2012), and both are nocturnal animals, sleeping in their shelters during the day. *Nyctereutes procyonoides* is the only canid species that shows hibernating behaviour (Kauhala & Kowalczyk 2011).

According to the Invasive Species Compendium, *Procyon lotor* and *Nyctereutes procyonoides* can be found in 20 and 33 countries in Europe, respectively, and patterns of genetic admixture have been recognised for both species (Drygala et al. 2016, Fischer et al. 2017, Nørgaard et al. 2017). Their geographical ranges overlap to a large extent in Europe; however, simultaneous sightings are rare. Only *Procyon lotor* uses human settlements, where it can cause damage to buildings and houses by looking for resting sites. In its native range in North America, but also in Japan, the species has caused substantial damage to crops (Ikeda et al. 2004, Beasley & Rhodes 2008). *Nyctereutes procyonoides* is not known for causing much economic loss (Kauhala & Saeki 2004, Mulder 2013).

One of the most important impacts these species have in their non-native range in Europe is their potential as health hazards for humans and animal livestock. *Procyon lotor* is the definitive host for the raccoon roundworm *Baylisascaris procyonis* and is also suspected to function as a reservoir host for West Nile virus (see review by Beltrán-Beck et al. 2012). *Echinococcus multilocularis*, rabies and canine distemper virus, and *Trichinella* are some of the pathogens found in *Nyctereutes procyonoides* (Sutor et al. 2014). Very recently, the susceptibility of *Nyctereutes procyonoides* for SARS-CoV-2 infection was reported (Freuling et al. 2020). Despite only few studies with firm evidence of negative impacts on native fauna, the predation behaviour of both species might become a threat to local populations of, e.g., waterfowl and amphibians (Salgado 2018, Fiderer et al. 2019, Dahl & Åhlén 2019).

As their diets and habitat use are very plastic, the only factor that might be limiting both species is climate. Climatically favourable areas have been predicted on a regional scale in Italy (Mori et al. 2015) and on a global scale (Louppe et al. 2019) for *Procyon lotor*, as well as for both species in Austria (Duscher & Nopp-Mayr 2017, Duscher et al. 2018), using various modelling approaches. We compare the native-range niches of both species in North America and East Asia with their non-native-range niches in Europe, based on eight bioclimatic variables. We hypothesised that the ecological niches of the two species would differ in Europe due to their different origins. In a second step, we modelled the climatic habitat suitability of both species in Europe using a maximum entropy (Maxent) niche modelling approach based on native-range data (Cunze et al. 2020, Lamelas-López et al. 2020, Raffini et al. 2020). The aim was to assess whether both species are already filling their climatic niches in Europe or whether they might expand their ranges in Europe into suitable areas that they have not yet filled.

METHODS

Occurrence records and bioclimatic variables

The Global Biodiversity Information Facility (GBIF) database contained 28258 records for *Procyon lotor* from 167 published datasets (GBIF.org 2019a) and 10459 records for *Nyctereutes procyonoides* from 57 published datasets (GBIF.org 2019b). The existence of different subspecies has been discussed in the case of both species (Nie et al. 2003, Hohmann & Bartussek 2018, Sun et al. 2019, Hong et al. 2020), but so far, no consensus has been reached. Therefore, we did not differentiate between potential subspecies. In addition, GBIF occurrences were overlaid with International Union for Conservation of Nature (IUCN) polygons for both species (Timm et al. 2016, Kauhala & Saeki 2016).

A global subset of bioclimatic variables (based on data from the years 1970 to 2000) was identified by a cluster analysis of dissimilarities derived from a Pearson correlation matrix ($D = 1 - |r_p|$; threshold $|r_p| < 0.7$) of all 19 available WorldClim bioclimatic variables (version 2.0; Fick & Hijmans 2017; Appendix S1). The data were downloaded with a spatial resolution of 5 arc minutes, and we applied a complete linkage cluster algorithm. The following eight bioclimatic variables were singled out among groups of highly correlated variables, and were considered ecologically relevant, easy to interpret, and without strong discontinuities in spatial pattern: bio02 – mean diurnal range; bio04 – temperature seasonality; bio05 – maximum temperature of the warmest month; bio06 – minimum temperature of the coldest month; bio14 – minimum precipitation of the driest month; bio15 – precipitation seasonality; bio18 – precipitation of warmest quarter; and bio19 – precipitation of coldest quarter.

We considered three study areas, comprising all recorded occurrences of the two species until December 2019: North America as the native range of *Procyon lotor* (-135° to -65° W; 5° to 55° N), Asia as the native range of *Nyctereutes procyonoides* (100° to 155° W; 15° to 60° N), and Europe as the non-native (introduced) range of both species (-15° to 65° W; 35° to 75° N; Appendix S2).

Ecospat

To characterise the climatic niches of the two species in their native and non-native ranges, we first applied the environmental principal component analysis (PCA-env) approach developed by Broennimann et al. (2012) using the R package ecospat 2.1.1. (Broennimann et al. 2016). This approach works in the two-dimensional gridded environmental space (250×250 grid), which is spanned by the first two axes derived from the PCA on the eight

bioclimatic variables. To be able to compare all three ranges (North America, Asia, and Europe), the PCA was carried out using the R function rcomp (scale = T, centre = T). Our choice of geographical background (Appendix S2) was based on two criteria: first, all occurrences of the species had to be included within the extent; and second, areas accessible to the species by natural dispersal from original occurrence points had to be possible (Hill et al. 2017).

Niche unfilling, niche expansion, and niche stability were used as niche parameters to compare the native-range and non-native-range niches for the two species (Guisan et al. 2014). Niche unfilling is the percentage of the native-range niche that is not (yet) occupied within the non-native range. A high niche unfilling can indicate restricted dispersal activities, leading to limitations in the current distribution. Niche expansion is the percentage of the non-native-range niche that is not covered by the native-range niche, and refers to climatic conditions under which the species occurs within the non-native range but not within the native range. Niche stability is based on the former two parameters and refers to climatic conditions experienced by species within the native and non-native ranges (niche stability = $1 - \text{niche expansion}$).

Maxent

We trained the Maxent models for both species with GBIF data of species' occurrences and all eight bioclimatic variables, each covering the native range. The coordinates of all records were adjusted to a spatial resolution of 5 arc minutes ($\sim 10 \text{ km} \times 10 \text{ km}$) to match the raster of the environmental variables, and accounted for only one occurrence record per grid cell to minimise spatial autocorrelation (Humphreys et al. 2019, Pearman et al. 2020, Smeraldo et al. 2020). For *Procyon lotor*, after removal of duplications, a total number of 6911 occurrences remained from North America, and 4863 (70%) and 2084 (30%) occurrence records were used for training and testing, respectively. A much smaller number of occurrence records were available after removal of duplications for *Nyctereutes procyonoides* from its native range in Asia, with 192 occurrence records, divided into 135 and 57 for training and testing. The models were trained on the respective native-range data of each species, because both species are still expanding their ranges and are not yet in equilibrium. Models trained only on data from the non-native range would therefore have underestimated the niche and areas with climatically suitable conditions, due to violation of the equilibrium assumption (Elith et al. 2010). We projected the models for both species onto Europe and transformed the continuous model outputs into binary habitat suitability maps using the threshold

that minimised the difference between sensitivity and specificity (Liu et al. 2013). To assess the environmental similarity between the native ranges and Europe, a Multivariate Environmental Similarity Surfaces analysis was carried out in Maxent. Negative values indicated where environmental conditions in Europe are dissimilar to those in the native range, and where extrapolation was therefore needed.

Maxent was used with its default settings, but with linear, quadratic, and product features and no hinge features (Cunze & Tackenberg 2015). The maximum number of iterations was increased to 50000 in order to ensure convergence. We used AUC (area under the curve; Fielding & Bell 1997) as a measure of model performance and calculated the average importance of the bioclimatic variables in the Maxent models for both species.

RESULTS

We displayed the geographical distributions based on available occurrence data of *Procyon lotor* and *Nyctereutes procyonoides* in their native ranges using the GBIF and IUCN database (Fig. 1). While GBIF occurrences of *Procyon lotor* match the IUCN dataset almost entirely, the IUCN data for *Nyctereutes procyonoides* extend far beyond the occurrence points documented in GBIF.

Ecospat

The first two axes of the PCA explain 65% of the total variance (PC1: 38%; PC2: 27%; Fig. 2), and niche plots were interpreted using the correlations between the two PCA axes and the bioclimatic variables.

The comparison of the native and non-native niche of *Procyon lotor* revealed no niche expansion (0.0012), but

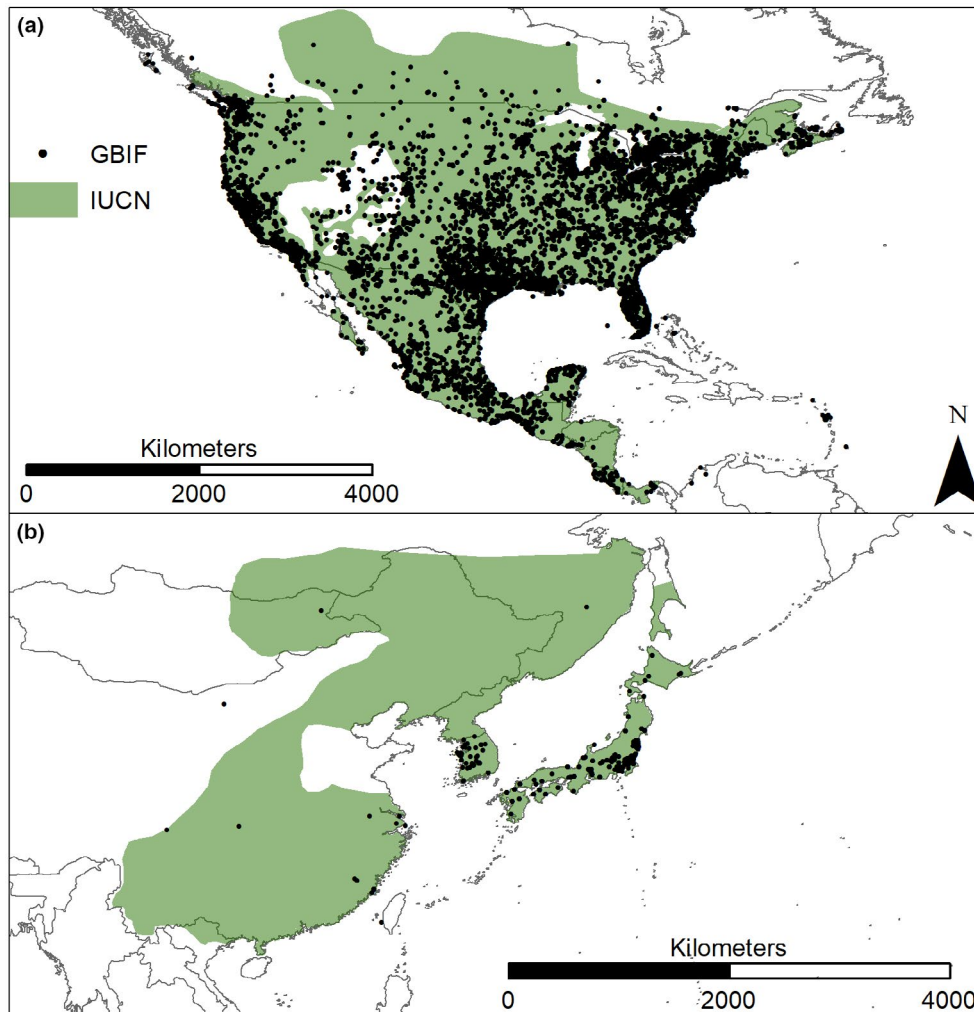


Fig. 1. Distribution data for (a) the raccoon *Procyon lotor* and (b) the raccoon dog *Nyctereutes procyonoides* in their native ranges in North America and eastern Asia, based on the GBIF (point data) and IUCN (polygon data) databases.

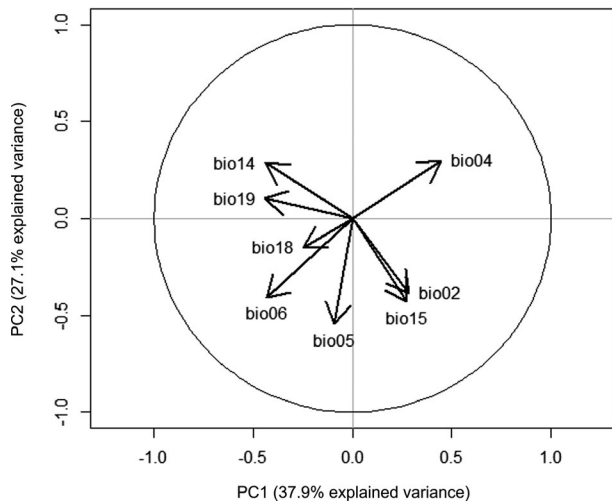


Fig. 2. Principal component analysis (PCA) of the eight bioclimatic variables, with PC1 axis explaining 38% and PC2 axis explaining 27% of the total variance. Variables are as follows: bio02 – mean diurnal range; bio04 – temperature seasonality; bio05 – maximum temperature of the warmest month; bio06 – minimum temperature of the coldest month; bio14 – minimum precipitation of the driest month; bio15 – precipitation seasonality; bio18 – precipitation of warmest quarter; and bio19 – precipitation of coldest quarter.

a high niche unfilling (0.7256) and niche stability (0.9988) in the non-native range in Europe. In contrast, comparison of the native and non-native niche of *Nyctereutes procyonoides* based on GBIF data suggests a niche expansion (0.6401), a high niche unfilling (0.9315), and a low niche stability (0.3599) in the non-native range (Fig. 3).

Comparing the patterns of both species in Europe, *Nyctereutes procyonoides* and *Procyon lotor* seem to be occupying climatic niches that largely overlap. The niche seems to be expanded towards 45° for *Nyctereutes procyonoides*: individuals of this species are occupying areas with larger seasonal fluctuations in temperature (bio04) and with lower minimum temperatures (bio06) than areas occupied by *Procyon lotor* (Fig. 3).

Maxent

The discriminatory capacity of the two models displays a good predictive performance, which is also reflected in the AUC values of the test data, with 0.730 for the *Procyon lotor* model and 0.963 for the *Nyctereutes procyonoides* model. The most important bioclimatic variable is the minimum temperature of the coldest month (bio06) for

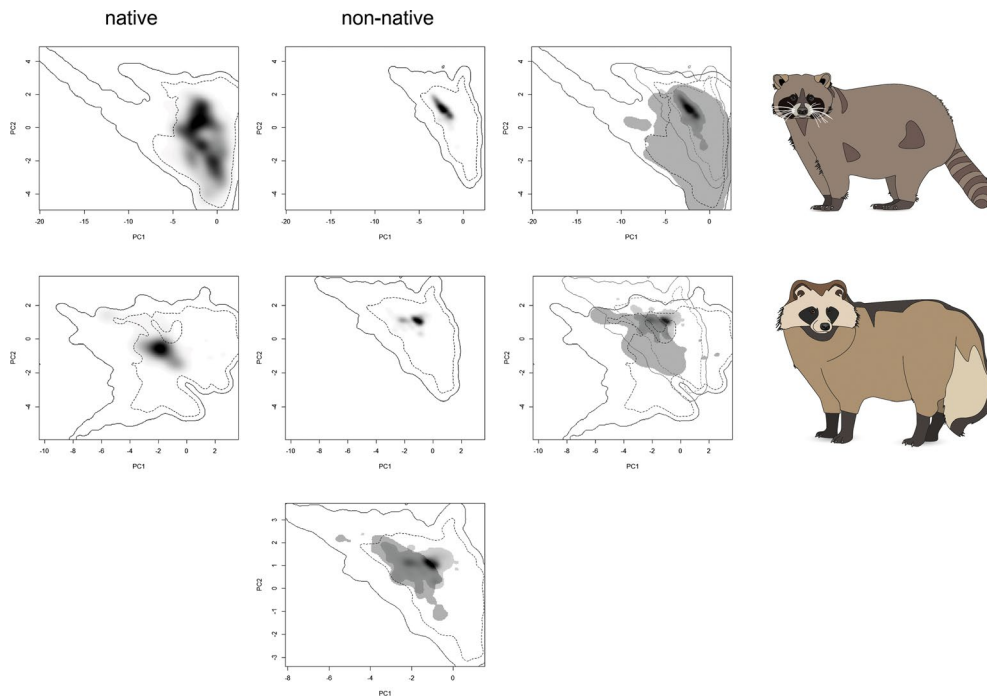


Fig. 3. Climatic niches in the native and non-native range of the raccoon *Procyon lotor* (top row) and the raccoon dog *Nyctereutes procyonoides* (middle row) based on GBIF data in the niche space spanned by the first two axes of the principal component analysis (PCA). Upper rows: realised niches are displayed as densities (black ‘clouds’) or shaded areas (light grey, non-native range only; medium grey, native range only; dark grey, both ranges). Bottom row: overlay of non-native niches displayed as shaded areas (light grey, *Nyctereutes procyonoides*; medium grey, *Procyon lotor*; dark grey, both species). Solid and dashed contour lines visualise the most common background environment, 100% and 50%, respectively. Figures were built using the R Package ‘ecospat’ version 2.1.1.

both species, followed by the maximum temperature of the warmest month (bio05) in the *Procyon lotor* model, and precipitation seasonality (bio15) and precipitation of the warmest quarter (bio18) in the *Nyctereutes procyonoides* model. All other variables contribute less than 10% in permutation importance (Appendix S3). The results of the Multivariate Environmental Similarity Surfaces analysis are provided in Appendix S4. No negative values were found for *Procyon lotor*, but in a small area on the west coast of Norway, results of the Maxent model seem to be largely uncertain for *Nyctereutes procyonoides*.

We transformed the continuous values between 0 and 1 for the modelled habitat suitability into dichotomous results by applying a threshold (equal test sensitivity and

specificity) of 0.629 for *Procyon lotor* and 0.133 for *Nyctereutes procyonoides*. The training-omission rate is 0.343, and the test-omission rate is 0.339 for *Procyon lotor*, and 0.037 and 0.088 for *Nyctereutes procyonoides*, respectively, in the native range. The projected binary climatic suitability models suggest similar ranges for both species in Europe, with a wide potential occupancy in Central Europe (Fig. 4). Differences appear to exist towards north-western areas, with suitable climatic habitats for *Nyctereutes procyonoides* in Ireland, the UK, and southern Sweden, and, in an easterly direction, reaching far beyond Poland and the Baltic states. *Procyon lotor* seems to find suitable habitats in all coastal areas but not be able to reach higher elevations, such as those of the alpine system.

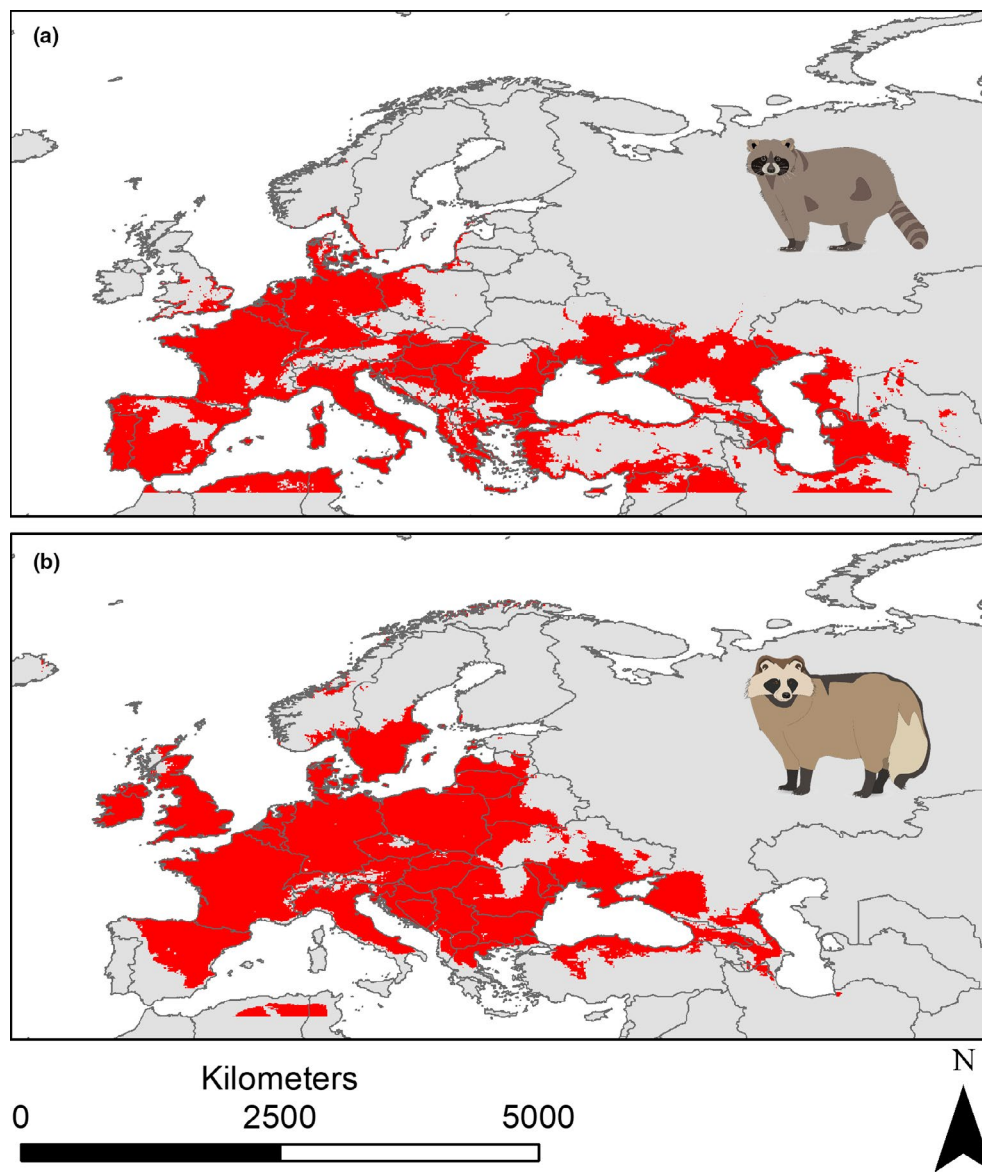


Fig. 4. Projected area of climatic suitability in Europe for (a) the raccoon *Procyon lotor* and (b) the raccoon dog *Nyctereutes procyonoides*.

The models were based on native occurrence data alone, and the projected habitat suitability in Europe fits the recorded presences well for both species, with one major exception of Finland and isolated data records in Russia for *Nyctereutes procyonoides*. Some single sightings outside the habitat suitability projections for *Procyon lotor* have been made in the UK, Ireland, and Poland. The large extent of suitable habitats without overlapping occurrence records reflects the high niche unfilling quantified in the ecospat approach.

DISCUSSION

The raccoon *Procyon lotor* and the raccoon dog *Nyctereutes procyonoides* are included on the EU's list of invasive species in Europe, and all member states are required to undertake actions to manage their populations and prevent and mitigate their negative impacts on native fauna and habitats (EU regulation No. 1143/2014). We modelled the native and non-native niches of these two mammals to assess their future invasion potential and projected climatic habitat suitability, in order to understand where climate might be a limiting factor for these species in Europe.

The high niche unfilling in Europe indicates that both species are limited in their current distribution in Europe; i.e., they experience climatic conditions in their native ranges similar to conditions that exist in Europe in areas that are not yet occupied by *Procyon lotor* or *Nyctereutes procyonoides*. Thus, there is a clear risk of these species spreading further and expanding their ranges in Europe beyond their present distribution. Despite originating from different continents and having different environmental backgrounds, the species' niches in Europe seem to be overlapping to a large extent. We based the models of the potential geographical distribution of both mammals in Europe on presence records from the native range alone, to avoid violating the equilibrium assumption (Elith et al. 2010). Both species are not yet in equilibrium and are still spreading in Europe, an observation supported by the results of high niche unfilling.

Overall, climatic factors alone do not pose great restrictions to the spread of *Procyon lotor* or *Nyctereutes procyonoides* in Central Europe. This is as expected, given that, from a physiological point of view, these two mammals do not rely on very strict and narrow temperature regimes, unlike aquatic life stages of mosquitoes or plant species that have specific optima and are very much restricted in their dispersal range by temperature, even on a micro-scale. However, species-specific physiological limitations or tolerances might explain why small differences in the distribution pattern between the two mammalian species exist, especially at the margins of their distribution.

In the case of *Nyctereutes procyonoides*, mountainous and alpine environments are included as suitable habitats in the projections, e.g. the Alps, Pyrenees, and Dinaric Alps. Regarding the habitat suitability of these specific regions, an almost opposite pattern presents itself for *Procyon lotor*. Colder temperatures and higher elevations do not offer suitable habitat for *Procyon lotor* in Europe, e.g. in Scandinavia, which supports modelling results from a previous study suggesting a low habitat suitability of the Italian Alpine regions (Mori et al. 2015). Warmer climate and higher elevations do seem to be acceptable for the species, as suggested by the projected habitat suitability in Spain and Portugal. In fact, although records were not included in the GBIF database, individuals of *Procyon lotor* have been sighted around Madrid (García et al. 2012). Elevation could be considered a limiting factor in the distribution of the two mammals, but might rather be an indirect predictor. Instead, snow cover and snow depth, which were not included as climatic variables in this study but have been described as relevant climatic components of the niche of *Nyctereutes procyonoides* in its native range (Seki & Koganezawa 2011) and non-native range (Duscher & Nopp-Mayr 2017), are proposed as substitutes, due to their strong correlation with elevation. Although the minimum temperature of the coldest month was identified as the most important variable for both species in the Maxent model, low food availability associated with cold weather during winter may pose bigger limitations to *Procyon lotor*, since *Nyctereutes procyonoides* is the only canid able to overwinter passively (Asikainen et al. 2004, Mustonen et al. 2007), a behaviour that may have contributed to its successful spread into Northern Europe (Kauhala et al. 2007, Kauhala & Kowalczyk 2011). Suitable habitats for *Nyctereutes procyonoides* are also projected to occur at locations with bigger seasonal differences in temperature, e.g. Eastern and Northern Europe.

Coastal areas and their prevailing climatic habitat conditions seem to favour occurrences of *Procyon lotor* equally in the south and north of Europe, but present less suitable habitats for *Nyctereutes procyonoides* in the south, from the Atlantic coast of Spain and along the entire Mediterranean coast as far as Greece and Turkey. The difference may be related to the inherent thermal physiological traits of the species. Our findings on the climatic regions favourable for *Procyon lotor* largely corroborate results of a recent study by Louppe et al. (2019). The authors used WorldClim version v1.4 based on data from 1950 to 2000 and chose slightly different climatic variables (bi01, 02, 10, 12), which might explain why small discrepancies in specific regions occur, e.g. projections in Ireland and the UK.

Suitable areas are projected to occur for both species in Western Europe, matching a large number of the GBIF

occurrence records for both species, e.g. in Germany and Denmark. Some isolated records of *Procyon lotor* falling outside the potential range could be sightings at the edge of their distribution, which had a higher chance of being reported to GBIF because they are unusual. *Procyon lotor* has not established itself yet on the British Isles, and sightings of individuals could be escapees or releases by pet owners near residential areas (Salgado 2018). Similarly, the projections based on presence records of *Nyctereutes procyonoides* in its native range in Asia fit the occurrence records in Europe relatively well, except for underestimating its distribution in Scandinavia, especially Finland. We believe that this underestimation is due to a sampling bias, i.e. insufficient distribution records for *Nyctereutes procyonoides* in the GBIF database so that it does not reflect the entire range currently occupied in Asia. This bias might equally explain why using native occurrence data of *Nyctereutes procyonoides* from the GBIF database in the ecospat approach yielded a niche expansion in Europe. Considering the much higher number of studies and the larger surveillance effort in North America and Europe compared with those in Asia (Meyer et al. 2015), this discrepancy in number of recorded presences in the GBIF database seems plausible. Single occurrence records in Russia might be linked to single introduction events where establishment failed in the past, and the higher AUC value for *Nyctereutes procyonoides* can be explained by its overall lower prevalence; i.e., fewer data points were used for its Maxent model than for *Procyon lotor*.

Large-scale climatic habitat suitability of the two invasive carnivores exists in Europe and is likely to expand under future climate change. Together with the risk of pathogen transmission to animal stocks and humans in urban environments, this is another strong supportive signal demonstrating that management action is required on local and regional levels if EU member states want to control or prevent further expansion of the two species (Beever et al. 2019). Different management options might need to be discussed and applied depending on the location, e.g. in areas with a large number of individuals, and in areas at the edge of their distribution. Hunting and trapping of individuals is already common practice in many countries, but efficiency is highly dependent on population densities and the type of traps used (Dahl & Åhlén 2017, Mazzamuto et al. 2020).

As a next step, models should incorporate land-use variables on a European scale in order to further differentiate and localise suitable and potentially overlapping habitats for both species (for land-use models applied to *Procyon lotor*; see Fischer et al. 2016, Germany; Duscher et al. 2018, Austria). Variables related to the influence of humans, such as population density or urbanisation, might also be considered (Srivastava et al. 2019). This would

help to identify the negative impacts of the two species, e.g. on co-occurring species in protected habitats, and would ultimately benefit the development of guidelines and control options for local stakeholders.

ACKNOWLEDGEMENTS

Illustrations were kindly prepared by Fanny Eberhard. The present study was financially supported by the German Federal Environmental Foundation (Deutsche Bundesstiftung Umwelt – DBU 35524/01). Open Access funding enabled and organized by Projekt DEAL.

REFERENCES

- Asikainen J, Mustonen A-M, Hyvärinen H, Nieminen P (2004) Seasonal physiology of the wild raccoon dog (*Nyctereutes procyonoides*). *Zoological Science* 21: 385–391.
- Beasley JC, Devault TL, Retamosa MI, Rhodes OE (2007) A hierarchical analysis of habitat selection by raccoons in northern Indiana. *Journal of Wildlife Management* 71: 1125–1133.
- Beasley J, Rhodes O (2008) Relationship between raccoon abundance and crop damage. *Human-Wildlife Conflicts* 2: 248–259.
- Beever EA, Simberloff D, Crowley SL, Al-Chokhachy R, Jackson HA, Petersen SL (2019) Social-ecological mismatches create conservation challenges in introduced species management. *Frontiers in Ecology and the Environment* 17: 117–125.
- Beltrán-Beck B, García FJ, Gortázar C (2012) Raccoons in Europe: disease hazards due to the establishment of an invasive species. *European Journal of Wildlife Research* 58: 5–15.
- Bertolino S, Sciandra C, Bosso L, Russo D, Lurz PWW, Febraro MD (2020) Spatially explicit models as tools for implementing effective management strategies for invasive alien mammals. *Mammal Review* 50: 187–199.
- Broennimann O, Di Cola V, Guisan A (2016) Package ‘ecospat’: spatial ecology miscellaneous methods. R package version 2.1.1. <https://CRAN.R-project.org/package=ecospat>
- Broennimann O, Fitzpatrick MC, Pearman PB, Petitpierre B, Pellissier L, Yoccoz NG et al. (2012) Measuring ecological niche overlap from occurrence and spatial environmental data. *Global Ecology and Biogeography* 21: 481–497.
- Courchamp F, Chapuis J-L, Pascal M (2003) Mammal invaders on islands: impact, control and control impact. *Biological Reviews of the Cambridge Philosophical Society* 78: 347–383.
- Cunze S, Kochmann J, Klimpel S (2020) Global occurrence data improve potential distribution models for *Aedes japonicus japonicus* in non-native regions. *Pest Management Science* 76: 1814–1822.

- Cunze S, Tackenberg O (2015) Decomposition of the maximum entropy niche function – a step beyond modelling species distribution. *Environmental Modelling & Software* 72: 250–260.
- Dahl F, Åhlén P-A (2017) *Information on measures and related costs in relation to species included on the Union list: Nyctereutes procyonoides*. Technical Note, IUCN, Gland, Switzerland.
- Dahl F, Åhlén P-A (2019) Nest predation by raccoon dog *Nyctereutes procyonoides* in the archipelago of northern Sweden. *Biological Invasions* 21: 743–755.
- Drygala F, Korablev N, Ansoerge H, Fickel J, Isomursu M, Elmeros M et al. (2016) Homogenous population genetic structure of the non-native raccoon dog (*Nyctereutes procyonoides*) in Europe as a result of rapid population expansion. *PLoS ONE* 11: e0153098.
- Drygala F, Stier N, Zoller H, Boegelsack K, Mix HM, Roth M (2008) Habitat use of the raccoon dog (*Nyctereutes procyonoides*) in north-eastern Germany. *Mammalian Biology* 73: 371–378.
- Duscher T, Nopp-Mayr U (2017) Species distribution modeling for the invasive raccoon dog (*Nyctereutes procyonoides*) in Austria and first range predictions for alpine environments. *Archives of Biological Sciences* 69: 637–647.
- Duscher T, Zeveloff S, Michler F-U, Nopp-Mayr U (2018) Environmental drivers of raccoon (*Procyon lotor* L.) occurrences in Austria - established versus newly invaded regions. *Archives of Biological Sciences* 70: 41–53.
- Elith J, Kearney M, Phillips S (2010) The art of modelling range-shifting species. *Methods in Ecology and Evolution* 1: 330–342.
- Engelmann A, Köhnemann B, Michler F-U (2012) Eine Frage der Saison – aktuelle Ergebnisse zur Nahrungsökologie des Waschbären (*Procyon lotor*) in der nordostdeutschen Tiefebene. *LABUS* 36: 47–62.
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37: 4302–4315.
- Fiderer C, Göttert T, Zeller U (2019) Spatial interrelations between raccoons (*Procyon lotor*), red foxes (*Vulpes vulpes*), and ground-nesting birds in a Special Protection Area of Germany. *European Journal of Wildlife Research* 65: 14.
- Fielding AH, Bell JF (1997) A review of methods for the assessment of prediction errors in conservation presence/absence models. *Environmental Conservation* 24: 38–49.
- Fischer ML, Salgado I, Beninde J, Klein R, Frantz AC, Heddergott M, Cullingham CI, Kyle CJ, Hochkirch A (2017) Multiple founder effects are followed by range expansion and admixture during the invasion process of the raccoon (*Procyon lotor*) in Europe. *Diversity and Distributions* 23: 409–420.
- Fischer ML, Sullivan MJP, Greiser G, Guerrero-Casado J, Heddergott M, Hohmann U et al. (2016) Assessing and predicting the spread of non-native raccoons in Germany using hunting bag data and dispersal weighted models. *Biological Invasions* 18: 57–71.
- Freuling CM, Breithaupt A, Mueller T, Sehl J, Balkema-Buschmann A, Rissmann M et al. (2020) Susceptibility of raccoon dogs for experimental SARS-CoV-2 infection. bioRxiv <https://doi.org/10.1101/2020.08.19.256800>.
- García JT, García FJ, Alda F, González JL, Aramburu MJ, Cortés Y et al. (2012) Recent invasion and status of the raccoon (*Procyon lotor*) in Spain. *Biological Invasions* 14: 1305–1310.
- GBIF.org (2019a) GBIF occurrence download. Global Biodiversity Information Facility. <https://doi.org/10.15468/dl.zobdp2>.
- GBIF.org (2019b) GBIF occurrence download. Global Biodiversity Information Facility. <https://doi.org/10.15468/dl.hf6w8p>.
- Guisan A, Petitpierre B, Broennimann O, Daehler C, Kueffer C (2014) Unifying niche shift studies: insights from biological invasions. *Trends in Ecology & Evolution* 29: 260–269.
- Hill MP, Gallardo B, Terblanche JS (2017) A global assessment of climatic niche shifts and human influence in insect invasions. *Global Ecology and Biogeography* 26: 679–689.
- Hohmann U, Bartussek I (2018) *Der Waschbär*, 4th ed. Oertel & Spörer, Reutlingen, Germany.
- Hong Y, Lee H, Kim KS, Min M-S (2020) Phylogenetic relationships between different raccoon dog (*Nyctereutes procyonoides*) populations based on four nuclear and Y genes. *Genes & Genomics* 42: 1075–1085.
- Humphreys JM, Murrow JL, Sullivan JD, Prosser DJ (2019) Seasonal occurrence and abundance of dabbling ducks across the continental United States: joint spatio-temporal modelling for the genus *Anas*. *Diversity and Distributions* 25: 1497–1508.
- Ikeda T, Asano M, Matoba Y, Abe G (2004) Present status of invasive alien raccoon and its impact in Japan. *Global Environmental Research* 8: 125–131.
- Jarić I, Courchamp F, Correia RA, Crowley SL, Essl F, Fischer A et al. (2020) The role of species charisma in biological invasions. *Frontiers in Ecology and the Environment* 18: 345–353.
- Jeschke JM, Strayer DL (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* 102: 7198–7202.
- Jones HP, Holmes ND, Butchart SHM, Tershy BR, Kappes PJ, Corkery I et al. (2016) Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences of the United States of America* 113: 4033–4038.

- Kauhala K, Saeki M (2016) *Nyctereutes procyonoides*. The IUCN Red List of Threatened Species 2016: e.T14925A85658776. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T14925A85658776.en>. Downloaded on 16 December 2019.
- Kauhala K, Holmala K, Schregel J (2007) Seasonal activity patterns and movements of the raccoon dog, a vector of diseases and parasites, in southern Finland. *Mammalian Biology* 72: 342–353.
- Kauhala K, Kowalczyk R (2011) Invasion of the raccoon dog *Nyctereutes procyonoides* in Europe: history of colonization, features behind its success, and threats to native fauna. *Current Zoology* 57: 584–598.
- Kauhala K, Saeki M (2004) Raccoon dog *Nyctereutes procyonoides* (Gray, 1834). In: Sillero-Zubiri C, Hoffmann M, Macdonald DW (eds) *Canids: Foxes, Wolves, Jackals and Dogs. Status Survey and Conservation Action Plan*, 136–142. IUCN, Gland, Switzerland and Cambridge, UK.
- Lamelas-López L, Pardavila X, Borges PAV, Santos-Reis M, Amorim IR, Santos MJ (2020) Modelling the distribution of *Mustela nivalis* and *M. putorius* in the Azores archipelago based on native and introduced ranges. *PLoS ONE* 15: e0237216.
- Liu C, White M, Newell G (2013) Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography* 40: 778–789.
- Louppe V, Leroy B, Herrel A, Veron G (2019) Current and future climatic regions favourable for a globally introduced wild carnivore, the raccoon *Procyon lotor*. *Scientific Reports* 9: 9174.
- Mazzamuto MV, Panzeri M, Bisi F, Wauters LA, Preatoni D, Martinoli A (2020) When management meets science: adaptive analysis for the optimization of the eradication of the Northern raccoon (*Procyon lotor*). *Biological Invasions* 22: 3119–3130.
- Melis C, Herfindal I, Dahl F, Åhlén P-A (2015) Individual and temporal variation in habitat association of an alien carnivore at its invasion front. *PLoS ONE* 10: e0122492.
- Meyer C, Kreft H, Guralnick R, Jetz W (2015) Global priorities for an effective information basis of biodiversity distributions. *Nature Communications* 6: 8221.
- Mill AC, Crowley SL, Lambin X, McKinney C, Maggs G, Robertson P, Robinson NJ, Ward AI, Marzano M (2020) The challenges of long-term invasive mammal management: lessons from the UK. *Mammal Review* 50: 136–146.
- Mori E, Mazza G, Menchetti M, Panzeri M, Gager Y, Bertolino S, Di Febbraro M (2015) The masked invader strikes again: the conquest of Italy by the Northern raccoon. *Hystrix, The Italian Journal of Mammalogy* 26: 47–51.
- Mulder JL (2012) A review of the ecology of the raccoon dog (*Nyctereutes procyonoides*) in Europe. *Lutra* 55: 101–127.
- Mulder JL (2013) The raccoon dog (*Nyctereutes procyonoides*) in the Netherlands – its present status and a risk assessment. *Lutra* 56: 23–43.
- Mustonen A-M, Asikainen J, Kauhala K, Paakkonen T, Nieminen P (2007) Seasonal rhythms of body temperature in the free-ranging raccoon dog (*Nyctereutes procyonoides*) with special emphasis on winter sleep. *Chronobiology International* 24: 1095–1107.
- Nie W, Wang J, Perelman P, Graphodatsky AS, Yang F (2003) Comparative chromosome painting defines the karyotypic relationships among the domestic dog, Chinese raccoon dog and Japanese raccoon dog. *Chromosome Research* 11: 735–740.
- Nørgaard LS, Mikkelsen DMG, Elmeros M, Chriél M, Madsen AB, Nielsen JL et al. (2017) Population genomics of the raccoon dog (*Nyctereutes procyonoides*) in Denmark: insights into invasion history and population development. *Biological Invasions* 19: 1637–1652.
- Pearman TRR, Robert K, Callaway A, Hall R, Lo Iacono C, Huvenne VAI (2020) Improving the predictive capability of benthic species distribution models by incorporating oceanographic data – towards holistic ecological modelling of a submarine canyon. *Progress in Oceanography* 184: 102338.
- Raffini F, Bertorelle G, Biello R, D’Urso G, Russo D, Bosso L (2020) From nucleotides to satellite imagery: approaches to identify and manage the invasive pathogen *Xylella fastidiosa* and its insect vectors in Europe. *Sustainability* 12: 4508.
- Salgado I (2018) Is the raccoon (*Procyon lotor*) out of control in Europe? *Biodiversity and Conservation* 27: 2243–2256.
- Seki Y, Koganezawa M (2011) Factors influencing winter home ranges and activity patterns of raccoon dogs *Nyctereutes procyonoides* in a high-altitude area of Japan. *Acta Theriologica* 56: 171–177.
- Smeraldo S, Bosso L, Fraissinet M, Bordignon L, Brunelli M, Ancillotto L, Russo D (2020) Modelling risks posed by wind turbines and power lines to soaring birds: the black stork (*Ciconia nigra*) in Italy as a case study. *Biodiversity and Conservation* 29: 1959–1976.
- Srivastava V, Lafond VMA, Griess V (2019) Species distribution models (SDM): applications, benefits and challenges in invasive species management. *CAB Reviews* 14: 1–13.
- Sun W, Yang Y, Li G-Y (2019) The complete mitochondrial genome of the raccoon dogs (Canidae: *Nyctereutes ussuriensis*) and intraspecific comparison of three Asian raccoon dogs. *Mitochondrial DNA Part B* 4: 670–671.
- Sutor A, Kauhala K, Ansorge H (2010) Diet of the raccoon dog *Nyctereutes procyonoides* — a canid with an opportunistic foraging strategy. *Acta Theriologica* 55: 165–176.

- Sutor A, Schwarz S, Conraths FJ (2014) The biological potential of the raccoon dog (*Nyctereutes procyonoides*, Gray 1834) as an invasive species in Europe—new risks for disease spread? *Acta Theriologica* 59: 49–59.
- Timm R, Cuarón AD, Reid F, Helgen K, González-Maya JF (2016) *Procyon lotor*. The IUCN Red List of Threatened Species 2016: e.T41686A45216638. <https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T41686A45216638.en>. Downloaded on 16 December 2019.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Cluster dendrogram based on dissimilarity with a matrix threshold of $|r_p| < 0.7$. One variable was chosen (circles) from groups of highly intercorrelated variables (dashed boxes).

Appendix S2. Global occurrence data for a) *Procyon lotor* and b) *Nyctereutes procyonoides*.

Appendix S3. Relative contribution (calculated as permutation importance in %) of bioclimatic variables to the Maxent models for *Procyon lotor* and *Nyctereutes procyonoides*.

Appendix S4. Multivariate Environmental Similarity Surfaces analysis for a) *Procyon lotor* and b) *Nyctereutes procyonoides*.