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# Species distribution modeling for the invasive raccoon dog (*Nyctereutes procyonoides*) in Austria and first range predictions for alpine environments

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**Abstract:** Species distribution models are important tools for wildlife management planning, particularly in the case of invasive species. We employed a recent framework for niche-based invasive species distribution modeling to predict the probability of presence for the invasive raccoon dog (Nyctereutes procyonoides) in Austria. The raccoon dog is an adaptive, mobile and highly reproductive Asiatic canid that has successfully invaded many parts of Europe. It is known to occur in Austria since 1963 and is now widespread in the northern and eastern parts of the country, but its population density remains low. With the help of a species distribution model we identified focal areas for future monitoring and management actions, and we address some management implications for the raccoon dog in Austria. We also determined the environmental predictors of raccoon dog distribution in this alpine country. Its distribution seems to be mainly limited by climatic factors (snow depth, duration of snow cover, winter precipitation and mean annual temperature) and is thus linked to elevation. Consequently, we assumed the Alps to be a barrier for the spread of the invasive raccoon dog in Europe; however, its ecological permeability is expected to increase with ongoing climate change.

**Key words**: raccoon dog; *Nyctereutes procyonoides*; species distribution model; MaxEnt; Alps

## INTRODUCTION

Understanding species-habitat relationships is a fundamental issue in landscape ecology, allowing for the formulation of specific management demands. For invasive alien species (IAS), hindcasting and forecasting range expansions as well as range shifts are high-priority research issues that support decisions in ecological management. Explicitly incorporating species' physiological limits and range-limiting processes provides a realistic approach for modeling and forecasting species' distributions [1]. This in turn might help to delineate focal areas for management where the spread of IAS should be prevented and negative effects minimized, or at least it may help to improve surveillance and monitoring of the species. Thus, understanding invasion dynamics is particularly important at the edges of IAS distributions or at potential barriers, as in the case of the raccoon dog (*Nyctereutes procyonoides*) in Austria. However, species distribution models for the raccoon dog (RD) in the European landscape are rare. Melis et al. [2] analyzed coarse scale habitat use and distribution in Norway and Sweden, based on telemetry studies and mechanistic habitat suitability models. Sutor et al. [3] and Drygala et al. [4] also used telemetry data for habitat analyses of RDs in German lowland study areas. However, for alpine surroundings, large-scaled approaches were lacking.

The raccoon dog is a medium-sized carnivore native to the Far East. It was released as a huntable furbearer in the western parts of the former Soviet Union between 1928 and 1955 [5]. As an opportunistic generalist, the RD is highly adaptable [6]. Studies of the introduced range of the RD subspecies *N. p. ussuriensis* showed that each monogamous pair can produce up to 16 pups per year with a mean litter size of about 9 pups per year [7]. In their first year,



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both males and females have been shown to disperse from their natal home ranges with a mean distance of 13.5 km in northeastern Germany [8], and 14 km (females) and 19 km (males) in southeastern Finland [9]. The maximum dispersal distance detected so far in juvenile RDs in invaded areas is 108 km in Germany [6] and 145 km in Finland [7]. Thus, the RD has a high potential for both rapid population growth and fast range expansion of approximately 37000 km$^2$ per year [5]. Accordingly, it has successfully invaded many European countries in the past [7] and is defined as an invasive species due to its vast spreading. In some parts of the invaded range, RD densities have increased exponentially [7] and in some areas, the species has become the most common carnivore.

In some areas of their invaded range it has been presumed that RDs could threaten local populations of waterfowl and amphibians [10]. However, it was concluded that little is known about its impact [7]. The most serious issue concerning RD invasion seems to be the transmission of diseases [7]. The RD is an important vector of rabies [11], fox tapeworm (*Echinococcus multilocularis)* [12] and other parasites and pathogens, constituting a health risk for livestock, wildlife and humans [7]. So far, there are no Austrian studies about its impact, but it is assumed to be a potential risk to Austrian native fauna [13].

In 2015, new legislation (EU Regulation No 1143/2014) on the prevention and management of the introduction and spread of IAS in the European Union (EU) entered into force. This regulation includes restrictions on bringing species of concern into EU territory, their keep, breeding, transport, release and use, or bringing to market. Furthermore, every member state is obliged to establish a surveillance system and institute effective management measures for those IAS of EU concern.

To date, the RD is not listed as a species of EU concern, but it is currently under discussion for listing as a species of concern. It is deemed to be a low-risk species in Belgium [14] and a moderate environmental risk in the Netherlands [15], while it is considered "potentially invasive" in Germany [16]. However, the DAISIE (Delivering Alien Invasive Species Inventories for Europe) network has listed the RD among 100 of the worst IAS in Europe (http://www.europe-aliens.org/speciesTheWorst.do; viewed February 2015). Since the development of IAS risk assessments is ongoing and the EU blacklist will be updated regularly, it remains uncertain how and to what extent this EU regulation will influence RD management at the national or local level. An attempt to eradicate the invasive RD in Europe is not promising due to its large-scale distribution [7,16]. Moreover, the implementation of a continental strategy concerning the RD is difficult due to its spread across different countries with diverse national interests [e.g. 17] and different hunting systems, but to list it as a species of EU concern could be a step towards the harmonization of national strategies. Nevertheless, the population of this adaptive and highly reproductive alien species must be controlled on national or regional levels in order to limit further range expansion and probable population increase, or at least to reduce its potential impact in protected areas. In Austria, RDs are shot and trapped all year long to reduce their presumed negative influence on small game species, especially waterfowl [7,10].

Our study aimed to identify regions where a further increase of RD relative probability of occurrence can be expected and in particular focuses on alpine surroundings. We further highlight where monitoring and management actions should focus; we have compared the predictors of the RDs distribution in Austria to results of previous studies in other regions and environments. Therefore, our predictive distribution model contributes to a better recognition of potential RD occurrence, thereby enhancing detection probabilities and supporting further modeling and management steps [18].

The invasive species distribution model we used is to some extent congruent with species distribution modeling (SDM) for rare species, as occurrence data are frequently incomplete due to low detection probabilities or unknown occurrences in both cases. Model accuracy shows an asymptotic increase with sample size [19], which is often small for introduced species at the beginning of an invasion, e.g. within scarcely filled niches. Facing a lack of reliable absence-data, we chose a presence-only approach (maximum entropy – MaxEnt) to explore RD occurrence within the novel alpine distribution range. MaxEnt supports presence-only data analyses. It has been proven to be robust in case of small sample sizes [20] and it shows good performance [21].

As recently proposed [22], niche-based invasive species distribution modeling, monitoring and management should comprise a 10-stage framework, including: (i) invasion characterization, (ii) objectives statement, (iii) assumption and uncertainty articulation, (iv) scale recognition and assignment, (v) predictor variable selection, (vi) modeling technique adoption, (vii) autocorrelation supervision, (viii) prediction, validation and mapping, (ix) management and monitoring, and (x) refinement. The implementation of this framework should increase the legitimacy and utility of SDMs over time [22]. In this paper, we considered the items of this framework for the raccoon dog in Austria as far as possible. Based on our modeling results we provide suggestions on the management and monitoring of the species. Future refinement and continued application of an adaptive SDM will assist in the detection of changes in RD invasion and the improvement of its management [22] in Austria and other alpine environments in general.

## MATERIAL AND METHODS

### Study region

Our study covers the entire territory of Austria with a size of 83879 km². Forests cover 48% of Austrian territory; a further 34% are agricultural areas [23]. Austria is comprised of different climatic regions, ranging from the Pannonian lowlands (with a low mean annual precipitation of 500-750 mm, a high mean summer temperature of 18-22°C and relatively cold winters with a mean temperature from -2 to 0°C) in the east, to oceanic higher alpine regions (low mean annual temperature from -6 to 4°C, high annual precipitation up to 2500 mm) in the western part of the country [23]. Austria is a mountainous country with nearly two-thirds of the area occupied by the Alps (with altitudes up to 3798 m above sea level). As the highest massif in Europe, the Alps are a potential barrier for the natural dispersal of some IAS.

### Invasion history and current distribution of the raccoon dog in Austria

Raccoon dogs have been sighted in the northeastern parts of Austria since 1963. A list of these sightings has been published [24], with the first proven records from 1983 (Mannshalm, district Zwettl, Lower Austria) and 1984 (Auersthal, district Gaenserndorf, Lower Austria). In the following decades, further records of RDs have been published [25,26] revealing a slight increase in their spread.

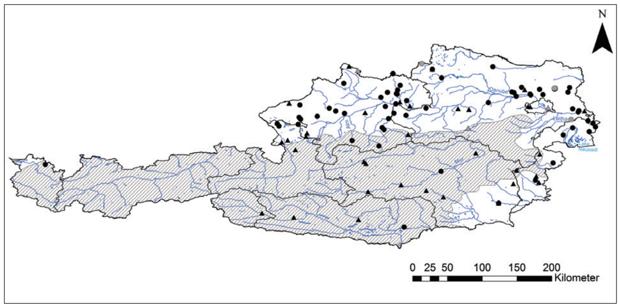


**Fig. 1.** Geographical distribution of proven raccoon dog records (●; ● juvenile) and uncertain raccoon dog records, e.g. sightings (▲; ▲ juvenile) in Austria (▨ alpine regions; ___ rivers and lakes) between 2000 and 2015.

In the present study, we collected 42 proven RD records (documented with photographs or carcasses), and 23 reports of RD trapped or shot or found dead between 2000 to 2015. Photographs were mainly obtained from private camera traps, non-systematically installed by hunters within their hunting grounds. Hence 65 verifiable records could be used to fit the distribution model. The geographical distribution of these records and additional 36 uncertain records (30 sightings and 6 tracks) are shown in Fig. 1. The verifiable records mainly stem from northern and eastern Austria (60 records). Only 5 verifiable records have been reported from the alpine regions and these are from lower altitudes (valleys or basins) in the Alps, as follows: Mur Valley (2004), Alm Valley (2009), Windischgarsten Basin (2011), Bregenz Forest (2014) and Klagenfurt Basin (2015). About half of the uncertain records, which we did not include in the SDM, were reported from alpine regions (17 records; Fig. 1).

For the first time, we documented juvenile sightings in Austria in 2010 and 2011 (in Lower Austria and Upper Austria), and recorded the presence of juvenile RDs in 2011 (district Gmuend, Lower Austria) and 2014 (district Gaenserndorf and district Bruck/Leitha, Lower Austria) (Fig. 1). Consequently, we can assume that there is a reproducing population of RDs in the northern and eastern parts of Austria that appears to be spreading westwards. So far, the population density remains at a low level [27] and ecological predictors of the establishment and spread of the RD in Austria are unknown.

## Sampling method

We collected raccoon dog records from the provincial museums, the Museum of Natural History in Vienna and from provincial hunting associations. We also sent questionnaires to an official of the Provincial Hunting Association of every district and to zoological preparators all over Austria. Additionally, we collected RD records from professional and nonprofessional hunters and citizens with the help of an online questionnaire. To support this investigation, we engaged in public relations by giving talks, writing articles and creating a project web site (www.enok.at). Thus, our data did not result from a consistent surveillance system but from random observations. In total, about 70% of proven records stemmed from hunters whose numbers and densities slightly differ among the provinces of Austria. Expressed in terms of hunting licenses per $km^2$ as a proxy of observer density, values range from 0.8 in Vorarlberg to 1.8 in Lower Austria, with a mean value of 1.5 for the entire Austrian state territory (Burgenland 1.7; Carinthia 1.2; Upper Austria 1.6; Salzburg: 1.4; Styria: 1.4) [28]). For SDM, we used proven records (documented by photograph or carcass) and reports of trapped or shot individuals, or those found dead from the period 2000 to 2015. Sightings without any proof and photographs of tracks (all of low quality and without indication of size) were treated as uncertain records.

## Species distribution modeling

Based on our presence-only dataset, we used MaxEnt for SDM. MaxEnt is a machine learning technique based on the principle of maximum entropy that uses environmental covariates from occurrence sites and a random sample of background data of the landscape of interest. In this way, an estimate of the probability density of covariates for occurrence sites within the landscape ($f_1(Z)$) is derived, where the one closest to the probability density of covariates across the landscape of interest ($f(Z)$) is chosen [29]. The distance of $f_1(Z)$ to $f(Z)$ is taken as relative entropy of $f_1(Z)$. MaxEnt estimates the distribution of a target species by iteratively minimizing the distance between $f_1(Z)$ and $f(Z)$. This is done by imposing constraints, where covariate means, estimated by $f_1$, converge closely to the mean value of occurrence sites. In MaxEnt, environmental covariates are weighted according to their contribution to model complexity, and the sum of weights, including regularization parameters, impede overfitting (i.e. too close matching of input data) [30]. However, in case of highly correlated variables, the contribution of these variables might be underestimated.

We modeled the probability of presence with MaxEnt version 3.3.3k [30]. Due to the small sample size, we chose a 10-times replication model and kept all other settings default. We first performed a run with all potentially relevant environmental variables (Table 1). As a measure of model performance, MaxEnt generates the mean area under the receiver operating characteristics curve (AUC) [31]. As the RD shows an opportunistic behavior with habitat preferences varying between study regions, we tried to find the best matching model for Austria with the highest AUC by deselecting variables with a low permutation importance.

## Predictor variable selection – the realized and fundamental niches of raccoon dogs

Recent ecological studies in other invaded countries in Europe have shown that RDs favor meadows, gardens and open woodlands with tall and abundant undergrowth in Finland [32], agricultural areas, wetlands, lower altitudes and shallow slopes in Sweden [33], and dense vegetation cover [34] or grassland and coniferous woods [3] in Germany. RDs used all habitat types opportunistically in their study region in Germany [4]. It was assumed that food is a key factor in habitat use [3], but its influence seems to be weaker in winter, when RDs reduce activity and use body-fat reserves. The latter authors furthermore hypothesized that a mixed landscape structure with tree or shrub cover and open habitat patches offers optimal conditions in terms of shelter and food availability for RDs.

Hence, RDs show a high plasticity in habitat use, and distribution limits appear to be primarily determined by climate [7]. In previous studies, it was shown in the native and introduced ranges that snow depth and winter temperature influence the activity

**Table 1.** Environmental variables (and their sources), used for modeling the probability of raccoon dog presence in Austria with MaxEnt.

| Type of variable | Variable acronym | Variable definition | unit | source |
|---|---|---|---|---|
| climate data (average of the period 1971–2000) | prec_year | sum of precipitation per year | l/m² | provided by ZAMG (http://www.zamg.ac.at) |
| | prec_winter | sum of precipitation between October and March | l/m² | |
| | prec_summer | sum of precipitation between April and September | l/m² | |
| | snowcover | number of days with full snow cover | days/year | |
| | snowdepth | average maximal snow depth | cm | |
| | ice_days | number of days with maximum <0°C | days/year | |
| | hot_days | number of days with maximum >=30°C | days/year | |
| | temp_jan | average temperature in January | °C | |
| | temp_jul | average temperature in July | °C | |
| | temp_year | average annual temperature | °C | |
| landcover data (based on CORINE landcover 2012) | clc_5cat | prevalent category: 1 = settlements, 2 = agricultural area/open landscape, 3 = forest, 4 = rock/permanent snow, 5 = water/wetland | category | provided by Environment Agency Austria |
| | prop_high | proportion of the grid cell that is covered with rock/permanent snow | surface ratio | |
| | prop_wet | proportion of the grid cell that is covered with water/wetland | surface ratio | |
| | prop_forest | proportion of the grid cell that is covered with forest | surface ratio | |
| | prop_open | proportion of the grid cell that is covered with agricultural area (incl. vineyard/pomiculture)/open landscape | surface ratio | |
| | prop_settle | proportion of the grid cell that is covered with settlements | surface ratio | |
| water distribution network | water | occurrence of waterbodies in the grid cell or not | category | |
| | water_cat | prevalent category of waterbodies: 0 = no water, 1 = lake, 2 = brook, 3 = river, 4 = river bank | category | |

and body conditions of RDs [35]. In [36], the authors assumed that an increased snow depth at higher latitudes can outline the border of RD expansion in northern Europe. Although most studies of its ecology were performed in low-altitude regions, altitude was shown to have an influence on the habitat use of Swedish RDs [33], and furthermore, it is considered to be an important factor influencing their distribution and abundance (subspecies *N. p. viverrinus*) in Japan (Seki Y, personal communication). Thus, both climate and altitude appear to drive RD invasions in Europe. However, since altitude can be considered a surrogate of other predictors (such as precipitation and duration of snow cover) and such indirect predictors might negatively affect transferability of models [22], we did not explicitly incorporate altitude into our modeling procedure and only considered assumed functional driving factors.

As shown by several authors [35,36], climate cues seem to determine the success of RD invasions, with precipitation, the duration of snow cover, snow depth as well as some temperature values and altitude [33] being components of the fundamental niche of this species. Moreover, studies on realized niches [3,4,32-24] identified preferences for different habitat types (e.g. land cover, vicinity of water bodies) with variations between study regions. Consequently, corresponding variables were chosen for the SDM (Table 1). Facing different climate zones, such as the inner-alpine regions with continental climate or pre-alpine regions with more oceanic climate within our study area, we considered potentially meaningful environmental drivers of RD distribution for modeling, even in case they were highly correlated over the entire Austrian state territory (e.g. snow depth and mean temperature in January).

## Spatial resolution

The environmental variables used for model fitting (Table 1) have been available in or were converted to an ESRI grid file format using the definition of the world geodetic system (WGS 1984). The geographical extension of these files corresponds to the Austrian extension of 46.3175728836 to 49.0460405292 north and 9.40258397741 to 17.2497471234 east. The size of the grid cells is 0.022549319 x 0.022549319. Therewith, every grid cell has a size of about 4 km², and can thus be assumed as a medium sized RD home range [9,33,35].

**Table 2.** Model performance (expressed as AUC-value) with different explanatory variables included, and permutation importance of environmental variables; the best candidate model with the highest AUC value is indicated in bold letters.

| mean AUC | Permutation importance of environmental variables | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | snow depth | snowcover | prec_winter | temp_year | temp_jan | clc_5cat | water_cat | prec_ summer | prop_open | prec_year | icedays | hotdays | prop_settle | water | prop_wet | prop_forest | temp_jul | prop_high |
| 0.84 | 51.0 | 7.1 | 9.6 | 5.6 | 6.5 | 2.6 | 3.2 | 2.3 | 4.1 | 2.6 | 2.9 | 0.8 | 0.8 | 0.6 | 0.2 | 0.1 | 0.1 | 0.0 |
| 0.85 | 55.3 | 11.9 | 9.2 | 5.0 | 4.8 | 2.8 | 3.5 | 2.1 | 2.1 | 1.8 | 1.4 | | | | | | | |
| 0.852 | 43.9 | 18.7 | 10.9 | 8.0 | 7.1 | 2.7 | 2.6 | 4.0 | 2.2 | | | | | | | | | |
| **0.854** | 52.0 | 20.5 | 10.5 | 8.4 | 3.2 | 2.4 | 3.0 | | | | | | | | | | | |
| 0.844 | 50.4 | 20.4 | 10.6 | 9.6 | 6.4 | 2.6 | | | | | | | | | | | | |
| 0.84 | 56.3 | 13.7 | 15.7 | 8.4 | 2.6 | | | 3.2 | | | | | | | | | | |

We converted all vector data (land cover data and water distribution network) to grid files using ArcGIS 10.1 (©ESRI). Thereby, we divided the land cover data into 5 categories (Table 1) and generated a grid file that provided the prevalent land cover category of each grid cell. Additionally, we generated one grid file for every land cover category showing the proportion of this category in each grid cell. As the representation of water bodies within the land cover data sometimes is not sufficient, we also produced one grid file showing the occurrence of water in each cell and another grid file showing the water categories (Table 1). For use in MaxEnt, we finally converted all grid files to ASCII grid format.

## RESULTS

Selecting the best candidate model for Austria based on mean AUC values and permutation importance of predictor variables (Table 2), we finally explained the probability of raccoon dog presence based on seven environmental variables with decreasing values of permutation importance: (i) snow depth, (ii) duration of snow cover, (iii) winter precipitation, (iv) mean annual temperature, (v) mean January temperature, (vi) prevalent land cover category and (vii) occurrence of water body categories.

The best candidate MaxEnt model that predicts RD presence in Austria has a mean AUC of 0.854 (±0.059). The resulting map (Fig. 2) shows that the probability of RD presence is comparably high (≥0.5) in the eastern and northern parts of Austria, in particular the Pannonian lowlands (with a probability of RD presence >0.8), the pre-alpine regions and the Austrian part of the Bohemian Massif. The predicted probability of RD presence is also comparably high in the Klagenfurt Basin (>0.8) in the very south of Austria, and in the northwestern edge of the Rhine valley and the Bregenz Forest (>0.7) in the west of Austria. According to these analyses, RDs are not expected to occur in the higher alpine regions.

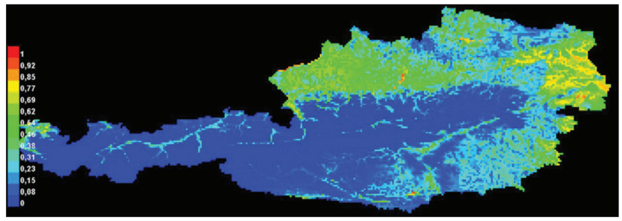

**Fig. 2.** Geographical representation of the predicted probability of raccoon dog presence in Austria (point-wise mean of 10 output grids).

Snow depth (permutation importance=52%) and duration of snow cover (permutation importance=20.5%) appear to be the most important environmental predictors of RD distribution in Austria (Table 3). Thus, no RD presence is expected in regions with a maximum annual snow depth of 150 cm and more, or in regions where the snow cover lasts 160 days or longer (Fig. 3).

Our results further indicate that RDs prefer a climate with mean annual temperatures (permutation importance=8.4%) of at least 1°C, and mean temperatures in January (permutation importance=3.2%) of at least -5°C, as well as relatively low winter precipitation (permutation importance=10.5%) (Table 3). In Austria, RDs seem to have a slight affinity to habitats close to rivers (probability of presence=0.88; permutation importance=3%), and wetland habitats (probability

**Table 3.** Permutation importance and predicted threshold or preference of included variables in the best candidate MaxEnt model for raccoon dogs in Austria.

| environmental variable | permutation importance [%] | threshold/ preference |
|---|---|---|
| snowdepth | 52 | the less the better, max 150cm |
| snowcover | 20.5 | the less the better, max 160 days/year |
| prec_winter | 10.5 | best at 200 l/m² |
| temp_year | 8.4 | the warmer the better, at least 1°C |
| temp_jan | 3.2 | the warmer the better, at least -5°C |
| water_cat | 3 | preference of rivers |
| clc_5cat | 2.4 | preference of wetland, avoidance of forests and rocky habitat |

of presence=0.76; permutation importance=2.4%), and they avoid forests as well as high altitude habitats with rocks and glaciers (both have a probability of presence=0.08; permutation importance=2.4%). The latter two habitat types are mainly situated in central Austria at higher altitude regions. In this regard, climate could be the real driver of habitat choice, as predictors of the realized niche seem to be of minor importance (permutation importance≤3).

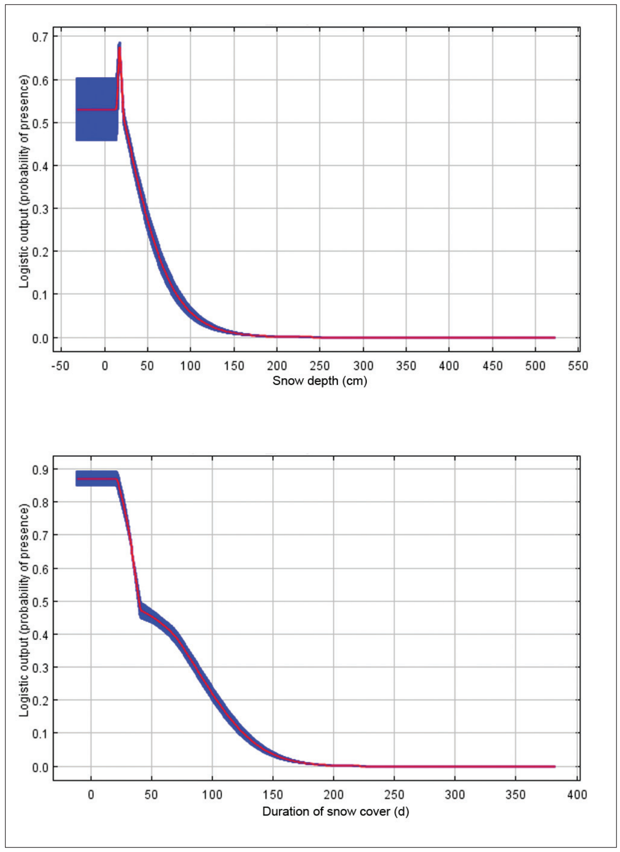


**Fig. 3.** Response curves showing the influence of (**A**) maximal snow depth (cm) and (**B**) duration of snow cover (days/year) on the probability of raccoon dog presence.

## DISCUSSION

### Realized and fundamental predictors of raccoon dog distribution

As raccoon dogs show high plasticity in their habitat selection [3,32], predictors of the realized niche seem to be of minor importance compared to predictors of the fundamental niche. The RD's preferences for river and wetland habitats, as noted in our study, can be explained by food abundance. Food is assumed to be a key factor of habitat choice [3], and amphibians, particularly aggregations of frogs, offer attractive food sources for RDs [10]. Furthermore, rivers and wetland habitats that favor RD presence are typically more abundant at lower altitudes, thus offering more favorable climatic conditions. In contrast, non-preferred rocky habitats and regions with the highest forest cover prevail at higher altitudes. Thus, the choice of land cover categories is probably influenced more by climatic cues.

Examination of the more important fundamental predictors of RD occurrence indicates that our findings are comparable to previously presented conclusions [7], wherein RDs live in areas where the mean annual temperature is above 0°C, the thickness of snow cover is <80 cm and the snow cover lasts <175 days. Accordingly, alpine regions are hardly affected by the RD invasion. In these regions, increasing altitudes are associated with increasing mean snow depth, increasing duration of snow cover and descending mean (annual and winter) temperatures [38]. To adapt to harsh environmental situations, RDs have at their disposal different wintering strategies to preserve energy, e.g. hibernating, denning, basking behavior or shifting of daytime activity [35,36,39]. Nevertheless, as assumed previously [7] and confirmed by our results, the distribution of the RD appears to be limited by climatic parameters that are clearly linked to altitude. Yet, the alpine habitats in Austria are evidently unsuitable for the raccoon dog and we consequently assumed that the Alps represent a barrier to the distribution and natural spread of RD in central Europe. As regards climate change, the ability of RDs to invade alpine regions might change due to predicted warming at higher elevations and large decreases in alpine snow amounts and its persistence below about 1500-2000 m a.s.l. [40].

**Assumption and uncertainty articulation**

Several factors could have affected our modeling results: first, our presence-only records are biased towards random observations rather than the results of a nationwide, continuous systematic sampling effort. Thus, they probably do not entirely reflect actual RD distribution and abundance as the frequency of these reports might be influenced by (i) differences in observer density, (ii) regional differences in communication networks, (iii) nonsystematic arrangement of hunters' traps, camera traps or other recording places due to reachability, and (iv) temporally different intensities of public relation activities. Contrasting records of RDs in Austrian provinces against densities of hunters per province (expressed in terms of hunting licenses per province), which were the main observer group with 70% of observations, no simple correlation can be assumed. For example, both terrain features and densities of hunters show a comparable order of magnitude in the provinces Salzburg and Styria [28], while the numbers of proven RD densities differ distinctly (Fig. 1). Thus, a lower number of observations cannot be explained by a lower number of observers, although it could be assumed that the presence of observers in a whole year cycle is lower in high-altitude regions as compared to lower altitudes. A critical assumption of presence-only (or presence-background) SDMs is that presence data are not spatially biased [41]. In fact, this is not true in many cases. Rather, the presence of data often merely reflects the presence of observers, which in turn might be affected by distances from human settlements, roads, or negatively correlate with altitude. In fact, a true absence of species is rarely recorded systematically. Therefore, such presence data do not reflect the entire range of environmental conditions where a species occurs (its realized niche), with this sampling bias pointing to models with a lower sensitivity (i.e. false negative rates) [42]. One option to adjust for sampling biases would be to estimate sampling efforts using logistic regression and to implement this information in further SDM steps [43]. However, intensifying monitoring efforts at locations of high probability of occurrence, as predicted by our SDM and by the establishment of a systematic surveillance system with camera traps [see 44] or consistent hunting bags, should be a primary goal in Austria in the coming years.

Overall, our raccoon dog observation data partially violate basic SDM assumptions, which is typical for many invading species occurrence data [22]. Therefore, (i) we assume that RDs have not reached species-environment equilibrium [45], particularly in the western areas of distribution in Austria; (ii) the information on realized niches in the invaded areas is incomplete [20]; and (iii) the habitat-species relationships and particularly range-limiting factors may differ between native areas and a novel range. The latter point seems to be of minor importance to our study as we only considered the environmental drivers of RD distribution within its European range and exclusively used the presence data from Austrian occurrences. However, evidence of successful reproduction as well as high-quality records of RDs in Austria provide important information for a first examination of the invasion patterns of this species, and for a prediction of its future distributions and the highly probable range-limiting factors.

Autocorrelation of environmental data can distinctly influence SDM output, as species occurrence can be driven by both environmental conditions at a given site and by the high degree of similarity between neighboring locations. In addition, established occurrences that are closer to an environmental equilibrium hold a higher potential of subsequent niche filling in neighboring locations than the initially invaded locations. Thus, adjacent pixels of SDM need not be regarded as being spatially and temporally independent [22,46]. As proposed previously [47], the effects of autocorrelation can be reduced by expanding the minimum distances between the presence points that are considered for SDMs beyond the scale of observed autocorrelation. In our study, grid cell size equals a medium-sized RD home range [9,33], which should ensure minor effects of spatial autocorrelation. Records within the study years are separated by at least 10 km (Fig. 1), except for one case when two single records from one year were made close together (1.8 km apart), but arose from two different individuals that were shot.

**Management challenges and future focal regions**

The current management of RD populations in Austria is determined by provincial hunting laws. It is permissible to shoot and trap RDs all year round. In Austria, hunting is a private enterprise as the right to hunt belongs to the landowner or it can be rented. Only a few hunters are specialized in trapping carnivores, and the shooting of RDs mainly happens by chance (e.g. while waiting for a wild boar at a feeding station). Furthermore, the overall interest in hunting or trapping carnivores is low as the fur can hardly be sold for a reasonable price. The efficiency of this type of management strategy within the context of a possible exponential increase in invasive RD populations is questionable. As a next step, both individual-based (VORTEX) and cohort-based (RAMAS) population models that simulate population growth rates and probabilities of extinction should be run to support management decisions and to prioritize actions at the meta-population level [48,49]. Hitherto, only one population viability analysis (VORTEX) has been run for RDs in Denmark [50], predicting marked expansions, with delays of only a few years for attaining carrying capacities when applying culling strategies. As discussed earlier [51], the situation in Europe is often drawn-out regarding the removal of vertebrates, and several eradication projects have been halted by public opposition. Likewise, because of the prevailing public opinion, it is unlikely that Austrian hunters will intensify hunting pressure or even consider an eradication campaign. However, responsible authorities could positively influence the success of IAS regulation by providing concrete support (e.g. by offering fur premiums or bounties) [52], and by increasing public awareness of IAS, specifically in the context of prevention and regulation.

Following our predictions, the Pannonian lowlands and pre-alpine areas in the north and east are regions with the highest probability of raccoon dog occurrence in Austria. In these regions, RD populations have already been established, as records are reported regularly and their reproduction has been confirmed. At present, RD density is low but there is a potential for an exponential increase as has been documented in other European countries [7]. Especially in eastern Austria, in the floodplain areas along the rivers Danube and Leitha, as well as in the vicinity of Lake Neusiedl, the predicted presence is high, and RDs are likely to establish relatively high densities. Several of these wetland habitats are protected national parks due to the presence of rare amphibians and waterfowl. Thus, future monitoring and management actions for the control of RD populations should mainly focus on these regions to reduce potential impacts.

**Implications for alpine neighbors**

In contrast to the eastern and northern lowlands, we do not expect significant increases in RD population densities in the alpine regions of Austria. Furthermore, our results suggest the Alps are a barrier for RD dispersal because of harsh climate conditions. This is relevant to the monitoring and management of RDs in neighboring countries. Despite the general barrier effect of the Alps, dispersal of RDs along alpine valleys could occur. Again, the barrier effect of the Alps on RD invasion could decrease due to climate change.

**Comparability of the IAS status in Europe**

A transparent and adaptive SDM presented in this study is a useful scientific tool that provides information about IAS for decision-makers at the regional, national and continental level. Beyond the existing recommendations of [22] for improving IAS management, the continual application and adaptation of an SDM framework could also facilitate comparisons between invasion dynamics of neighboring countries and extended risk mapping. This type of investigation helps to identify areas endangered as a result of the establishment and spread of IAS, as well as areas where IAS are likely to occupy in the near future [53]. Countries or regions will thereby be able to establish alarm lists. Cross-border collaboration is pivotal for the success of the EU regulation on IAS prevention and management [52]. The description of both actual and potential distributions, the spread and magnitude of impact, is defined as a minimum standard within the framework for the identification of IAS that are of concern to the EU [54]. Consequently, a transparent and adaptive SDM can also provide essential information for national and EU-wide risk assessments. Certainly, there is a clear need for schematic screenings of invasive species [14] in order to quantify and categorize impacts and to improve management priorities [55].

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