Environmental drivers of raccoon (*Procyon lotor* L.) occurrences in Austria – established versus newly invaded regions

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Abstract: As we are faced with the imminent spread of the raccoon (*Procyon lotor* L.), a successful and highly adaptable invader in Europe, it is necessary to identify the drivers of its distribution and focal areas of its future management. Being an omnivorous species, raccoons can exert considerable influence on prey species of various taxa. Species distribution models for this invasive species can be useful tools for its management. Using a presence-only model (MaxEnt) based on environmental variables selected by raccoon experts, the presence of raccoons in Austria was predicted. Core areas of raccoon colonization are mainly located in and around cities and river valleys. Identified ecological drivers of raccoon distribution comprise climate and land-cover variables, with temperature parameters (e.g. the number of hot days, mean January temperature), the proportion of coniferous forests, settlements and elevation mainly influencing the model output. The importance of habitat parameters changes with the stage of invasion. In Austria's established regions, the probability of raccoon presence was best predicted by variables chosen by an expert of the raccoon's native range, while the predictors chosen by an expert in its introduced range better reflected the situation in recently invaded regions. The significance of climate and land cover in understanding the probability of raccoon presence was shown.

Key words: *Procyon lotor* L.; species distribution modeling; MaxEnt; biological invasion; invasion stage

INTRODUCTION

The common raccoon (*Procyon lotor* L.) of North America is a superb example of an invasive species that has the potential to be enormously successful and thus detrimental. It readily adapts to a great variety of environments. Because of its ability to thrive in diverse habitats, the raccoon has one of the widest distributions of any North American mammal. It is also clear that the raccoon can prosper in much of Europe and Japan as well [1-3], posing distinct challenges for endemic conservation targets there. Its broad omnivory, opportunistic behavior and keen intelligence combine to make the raccoon a rather potent invasive species [4].

In Europe, the introduction of the raccoon as a huntable furbearer began in the first half of the 20th century in Germany [5-7]. As a result of such deliberate introductions for hunting, as well as releases and escapes from fur farms and recently escaped pets, raccoons have become widely distributed on the European mainland [8]. In Austria, the first immigrating raccoon was trapped in the vicinity of the Austrian-German border in Salzburg in 1974 [9]. Isolated records from different parts of eastern Austria in 1930 [10], 1972 and thereafter [9], as well as from Tyrol in 1993 [9], are assumed to have been generated by released or escaped raccoons and were complemented by immigrants from the northwest.

Whereas some introduced species do not become established due to low numbers of individuals and genetic bottlenecks, the introduction of high numbers of individuals over the course of consecutive, distinct events is more common [3]. As a result, the genetic diversity of introduced populations, e.g. for American Mink in Europe, might even exceed that of native populations [11]. While [3] found a low genetic diversity of mitochondrial markers in Polish raccoons and attributed this to the low number of individuals introduced, raccoons in Germany reached a high genetic diversity due to multiple introduction events and the admixture of source populations [12]. Genetic diversity is one of the key factors influencing the establishment and spread of nonindigenous species as well as the evolution of invasiveness [13].

As an omnivorous species, the raccoon may exert considerable influence on the prey species of differing taxa [1], and it has shown to be a vector of zoonoses [14,15] and contaminants [16] in its native range. However, several previous studies [17-19] have revealed a limited parasite fauna and thus a minor epidemiological impact [20] of the raccoon in Europe. Raccoons have been implicated in the predation of rare amphibians and reptiles [21]. In addition, they are known to compete with several owl species for hollow trees [2,21]. Thus, the raccoon is listed as a species of European Union concern (EU regulation 2016/1141) and its management is generally regulated by EU law (Regulation 1143/2014).

As described by [3], optimal raccoon habitats supporting high densities of this species may yield source populations for further invasion steps. Hence, management strategies should concentrate explicitly on areas of new colonization. However, raccoons might also inhabit suboptimal habitats at lower densities. It is important to know the drivers of raccoon invasions, the potential habitats, as well as the barriers for their expansion [22] to predict further changes in their distribution and to delineate focal areas for high-priority management.

In general, raccoon distribution, activity and status are influenced by a multitude of factors and processes: food and water availability [23-25], the supply of resting sites and breeding resources (e.g. the availability of high-quality den sites; [26]), landscape fragmentation and landscape changes [23,27], and the occurrence of barriers and the degree of urbanization [24,28,29] can all help to explain observed occurrences or abundances of raccoons. Furthermore, behavioral factors, density-dependent processes affecting habitat selection [30], source-sink situations [3], intraguild interactions (e.g. resource competition; [31], mate choice behavior [32]), predation by large carnivores [33] and the habitat-dependent prevalence of diseases [34] might each shape the landscape of colonization. In any case, the male-biased natal dispersal of raccoons [35-37] involves long dispersal distances and times during the early phase of colonization, and male dispersers only become established in areas with potential mates. As a result, many suitable habitats may not become occupied by raccoons at this stage [38].

Two crucial stages of invading species should be distinguished: the phase of establishment and the phase of spread into further new areas [39]. During both phases, the realized ecological niches may differ markedly [40]. While a species might be classified as specialist at its early phases of invasion, it may become a generalist in subsequent stages.

Consequently, studies involving native or established occurrences of raccoon are not comparable to those from newly invaded areas. Previous invasive species distribution models (iSDMs) in the core area of the European raccoon population [41] and at the southern border of its current distribution range [42] revealed that either land-cover data or climate data explained raccoon distribution. Furthermore, the habitat preferences of alien species can spatially vary across landscapes and depend on the stage of colonization, with less favorable habitats only being occupied when comparably high population densities are reached [41,43]. Studies of other invasive species have provided indications that including distribution data both from native and invasive ranges might yield better iSDMs than models relying solely on data from native ranges [44].

Hitherto, several approaches have been applied to exploring the spread and occurrence of raccoons and predicting their potential future areas of colonization. Basic data have been gained from telemetry studies [16,24], DNA genotyping [45], systematic records using scent stations, spotlight and latrine surveys,

track surveys or camera traps [27] and nonsystematic records (e.g. hunting bags, sightings, trappings, camera trappings, road-kills [41,43,46]). Using these variables, relative abundance calculations (e.g. hierarchical Bayesian approaches [47]), presence-absence approaches (logistic regression [27,41]), presence-only functions (e.g. ecological niche factor analysis (ENFA), maximum entropy (MaxEnt), outlying mean index analysis [28,42,43]) as well as dispersal models [41,45] have been employed for invasive species distribution modeling (iSDM). Whereas presence-absence analyses might be meaningful within native distribution ranges of species [27], they might not be easily applied to areas of current spread, as absence does not stringently reflect a lack of appropriate habitats, but might be better explained by stochastic events (e.g. releases) and temporal dimensions (e.g. the chronological development of the invasion front, consecutive filling of niches). Thus, iSDM frequently deals with presence-only data and incomplete occurrence data due to low or unknown detection probabilities. However, model accuracy does show an asymptotic increase with sample size [48].

In our study, we explored recent occurrences of raccoons in Austria and predicted the probability of their presence by a MaxEnt model utilizing data on land cover and climate. It has been shown by several authors that MaxEnt outmatches other comparable approaches when predicting invasive species distributions [44,49]. As stated by [50], explaining and predicting distributions of invasive species should consider the invasion stage (currently invaded vs. established ranges). Consequently, our study area was subdivided into regions with an established raccoon population and recently invaded regions. Expert-based definition of predictors of species occurrences is an accepted assumption in species distribution modeling [27,51,52]. Considering both established occurrences and areas of current invasion, environmental predictors chosen by an expert of the raccoon's native range (USA) for iSDM of established occurrences in Austria, and predictors assumed by an expert of the raccoon's introduced range (Germany) for iSDM in invasion zones were used. We compared the performance of models and hypothesized that raccoons show different realized ecological niches at different stages of their colonization. We thus expected that the assumptions of the native range expert should better predict raccoon occurrences in established regions in Austria and that those of the introduced range expert should yield better iSDMs for regions recently invaded by raccoons.

MATERIALS AND METHODS

Study region

Our study spans the entire territory of Austria with a size of 83879 km². Forests cover 48% of this nation and 34% are agricultural areas [53]. Austria comprises different climatic regions, ranging from the Pannonian lowlands (low precipitation with high summer temperatures but cold winters) in the east, to the higher alpine regions (low annual temperature and high precipitation) in the western parts of the country [53]. Austria is a mountainous country with nearly two-thirds of the area being occupied by the Alps (altitudes up to 3798 m above sea level). Being the highest massif in Europe, the Alps are a potential barrier for the dispersal of some IAS and are assumed to be a barrier for the raccoon [42].

For our modeling approach, Austria was subdivided into regions with established raccoon populations and recently invaded regions. All raccoon records (excluding escapees) documented in Austria until 2000 [10] were subsequently mapped. These areas, including a buffer radius of two kilometers, were defined as regions of established raccoon occurrences and the rest of the Austrian territory as the region of a recently ongoing invasion (i.e. more recent records since 2001).

Data collection

Proven raccoon records (documented with photographs or carcasses) were collected as well as sightings or reports of raccoons shot, trapped or found dead between 2000 and 2015. Provincial museums, the Museum of Natural History of Vienna and the provincial hunting associations were asked for raccoon records. Additionally, questionnaires were sent to an official of the Provincial Hunting Association of every district and to zoological preparators throughout Austria, and additional data were collected with an online questionnaire. To support this survey, we

engaged in public relations by giving talks, writing articles and creating a project web site (www.enok.at). Every record and its corresponding location was documented within an ArcGIS 10.1 (©ESRI) database.

For our iSDM, records reported twice, records of obviously escaped pets and zoo animals, and doubtable tracks were excluded. Finally, only one record per grid cell (of approximately 4 km²) was considered to avoid autocorrelation. [21] define the status of an alien species as "established" if the species lives in a distinct area for a long period of time and reproduces there without human support. According to [54], alien species become "established" when they survive in a distinct area for more than 25 years or form self-sustaining units that survive and reproduce for two consecutive times (i.e. three subsequent generations). Considering a typical start of reproduction of raccoons at an age of one (females) and two (males) years [1] and a maximum lifespan of 10-15 years in the wild [38], known occurrences for more than 15 years match the definition of established populations. In Austria, records of raccoon presence go back to the 1970s, covering a time span of more than 40 years. Based on the above definitions, we distinguished "established" (records until 2000 excluding escapees [10]) and "newly invaded" regions for raccoons in Austria and addressed the niches of both status classes. Our iSDM was based on 136 recent raccoon records (Table 1) in 127 grid cells throughout Austria with 101 grid cells being classified as established regions and 26 grid cells classified in the recently invaded regions (Fig. 1).

Invasive species distribution modeling

Based on our presence-only dataset, MaxEnt was used for iSDM [55,56] as it has been shown to be particularly suitable for invasive species [44,49]. MaxEnt is a machine learning algorithm based on the principle of maximum entropy [57] that uses environmental predictors from occurrence sites and a random sample of background data of a given landscape of interest. Thereby, an estimate of the distribution probability is derived by a set of constraints being inferred from presence sites. By means of these constraints, expected values of environmental predictors converge as closely as possible to the empirical mean of the occurrence sites of the respective predictor. Facing a set of distri-

Table 1. Categorization of collected records.

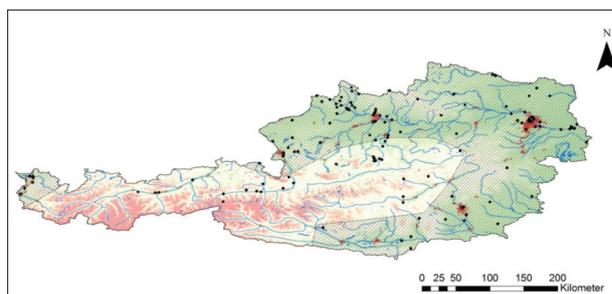| Category		Classification	Number of records involved
1		proven records, e.g. pictures of an animal, carcass, or tissue samples	45
2		pictures of track	2
3a	sightings	reports of a shot animal, trapped or found dead (without proof)	20
3b		sightings by experts (without proof)	24
3c		sightings (without proof)	45
4		records of obvious escapees, e.g. pets (with or without proof)	/

Fig. 1. Geographical distribution of raccoon records (•) outside (without shading) and inside Austria's established regions (▨)

butions, which potentially satisfy these constraints, MaxEnt selects the one closest to a uniform distribution, i.e. maximization of entropy [58].

Probabilities of presence (PP) were calculated with MaxEnt version 3.3.3k [55]. Due to the small sample size, a 10 times replication model, while keeping all other settings as default, was chosen. As a measure of model performance (discrimination accuracy), MaxEnt generates the mean area under the receiver operating characteristics curve (AUC; [55]).

For MaxEnt calculations, three different combinations of variables were used: (i) potential predictors chosen by the expert in raccoon native range, (ii) potential predictors chosen by the expert in raccoon introduced range, and (iii) the entire set of predictors (Table 2). For the first step, all chosen variables were used, irrespective of their correlative status to fully represent the experts' choices, respectively, even if they contained partially redundant variables. In a second step, correlations between the environmental predictors were tested and one of two highly correlat-

Table 2. Set of environmental predictors, indicating the variable selection by a native-range raccoon expert (a) and by an introduced-range expert (b).

Variable	Name of layer	Content of layer	Unit	Data source	Variables chosen by an expert of the	
					Native range (a)	**Introduced range (b)**
climate data (average of the period 1971 - 2000)	prec_year	sum of precipitation per year	l/m²	ZAMG	X	X
	prec_winter	sum of precipitation between October and March	l/m²		X	
	prec_summer	sum of precipitation between April and September	l/m²		X	X
	snowcover	number of days with full snow cover	days/year			X
	snowdepth	average maximal snow depth	cm			X
	ice_days	number of days with maximum < 0° C	days/year		X	
	hot_days	number of days with maximum >= 30 °C	days/year		X	
	temp_jan	average temperature in January	°C		X	
	temp_jul	average temperature in July	°C		X	
	temp_year	average annual temperature	°C		X	
altitude	dem	digital elevation model (from airborne laser scan)	m			X
land cover data	prop_settle	proportion of the grid cell that is covered with settlements	surface ratio	CLC 2012 (by Austrian Environment Agency; AEA)	X	X
	prop_decidforest	proportion of the grid cell that is covered with deciduous forest	surface ratio		X	X
	prop_conifforest	proportion of the grid cell that is covered with coniferous forest	surface ratio		X	X
	prop_otherforest	proportion of the grid cell that is covered with other forest (mixed, forest shrubs transition)	surface ratio			X
	prop_openarea	proportion of the grid cell that is covered with agricultural area/open landscape	surface ratio		X	X
	prop_vinepomi	proportion of the grid cell that is covered with vineyard/pomiculture	surface ratio		X	X
	prop_wetland	proportion of the grid cell that is covered with water/wetland	surface ratio		X	X
	prop_rocksnow	proportion of the grid cell that is covered with rock/permanent snow	surface ratio		X	X
water distribution network	water	occurrence of waterbodies occur in the grid cell	category (0/1)	AEA	X	X

ing predictors was omitted (correlation coefficients of 65% or higher [59]). Subsequent calculations were run with all possible combinations of non- or lowly correlating variables, respectively. Accordingly, the resulting models comprised a subset of variables of the original expert's choice (Table 4).

The environmental variables used for model fitting (Table 2) have either been available in ESRI grid file format or were converted accordingly using the software ArcGIS 10.1 (©ESRI) and 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 0.0225 x 0.0225 (approximately 4 km²). For use in MaxEnt, all grid files were finally converted to ASCII grid format. iSDM was done by differentiating the raccoon's established regions (A), recently invaded regions (B) and the entire territory of Austria (C), and by modeling each of these with the variables chosen by the expert of the native range (a), with the variables chosen by

the expert of the introduced range (b) and all variables (full model, (c)). Calculations were based on the hypothesis that models fed with the predictor set (a) would perform better for region A (in terms of AUC value) than for region B and vice versa. Additionally, the model settings a-A and b-B were expected to be superior to model settings c-A and c-B, and to the models for the entire nation. The relative importance of each potential driver of the raccoon distribution was evaluated by the permutation importance (PI) value [55]. Thereby, the values of the variables were changed randomly by MaxEnt, exploring their influence on changes in model output.

RESULTS

Comparison of MaxEnt models

For the entire territory of Austria, the model based on the native expert's choice of variables (a) performed best (AUC 0.793; Fig. 2), followed closely by the model fed with the variables chosen by the introduced-range expert (b) (AUC 0.790) and the full model (c) (AUC 0.786) (Table 3). The resulting map shows the highest probability of presence in big cities and in large river valleys (Danube, Rhine, Inn, Salzach, Mur, Drau) (Fig. 2). Furthermore, the predicted probability of presence was relatively high along the northern border of the Alps, e.g. in the Vienna Woods, as well as in the Muehl- and Innviertel in the northwest and in the Klagenfurt and Graz basins in the south.
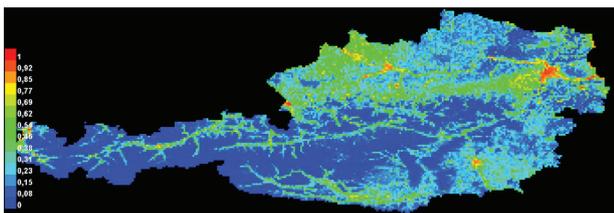

Fig. 2. Probability of raccoon presence in Austria based on variables chosen by a native-range raccoon expert

Model performance decreased when differentiating the regions A and B (Table 3). Within regions of assumed established raccoon populations, once more the model involving the entire variable choice of the native-range expert (i.e. model a-A) showed the highest AUC value (0.759) (Table 3). In contrast, for regions recently invaded by raccoons, the full set of variables chosen by the expert of the introduced range (model b-B) yielded the best AUC value (0.776).

MaxEnt models with subsets of (non- or lowly correlating) environmental predictors

Accounting for redundancy of highly correlating variables, MaxEnt was run with all possible combinations of non- or lowly correlating variables (Table 4), both for the expert choices of the native range (a) and for the expert choices of the newly invaded/introduced range (b). Thereby, regions A, B and the entire state territory (C) were considered again.

For regions with established raccoon populations (A) the highest AUC (0.753) was reached when including all land-cover variables (excluding the proportion of rocks and permanent snow cover), the occurrence of water bodies, the yearly sum of precipitation and the average temperature in January (model 2-A; Table 4). This subset of variables is based on the choice of the native-range expert. The variables that mostly influenced the calculated probability of presence in this particular model are the proportion of coniferous forests (PI=19) and the mean temperature in January (PI=18.7). While the probability of presence decreases with an increasing proportion of coniferous forests, it is positively correlated with the average January temperature (Fig. 3).

In the case of regions recently invaded by raccoons (B), the model involving the following variables performed best (AUC 0.795): land-cover data (excluding the proportion of rocks and permanent snow cover), the water network and altitude (model

Table 3. AUC values of models for different regions (A-C) with different sets of predictors (a-c).

Predictors/regions	Established regions (A) (records in 101 grid cells)	Recently invaded regions (B) (records in 26 grid cells)	Whole Austria (C) (records in 127 grid cells)
(a) chosen by a native-range expert	Model a-A: 0.759	Model a-B: 0.755	Model a-C: 0.793
(b) chosen by an introduced-range expert	Model b-A: 0.748	Model b-B: 0.776	Model b-C: 0.790
(c) all (full model)	Model c-A: 0.751	Model c-B: 0.761	Model c-C: 0.786

Table 4. Combinations of non- or lowly correlating variables, referring AUC values of MaxEnt models and permutation importance (PI) of variables for established occurrences (A), newly invaded regions (B), and the entire state territory (C); choice of expert for the native range (a) on the left (model # 1 – 8) and choice of expert of introduced range (b) on the right (model # 9 – 11). The best candidate model (highest AUC) per region is indicated in red. The trend of the response curves of the different models are marked with "+" for positive correlation, "-" for negative correlation and "+/-" for a unimodal curve.

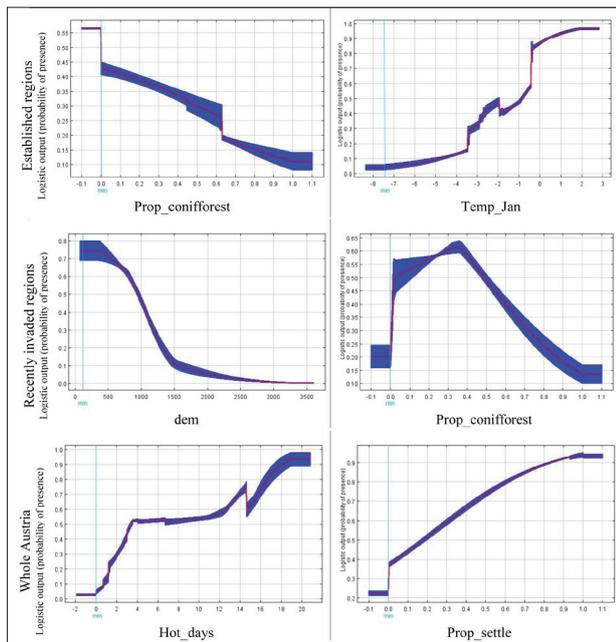| Variables / model #	Based on the native-range expert's choice (a)								Based on the introduced-range expert's choice (b)		
	1	2	3	4	5	6	7	8	9	10	11
prec_year	x	x									
prec_winter			x	x							
prec_summer					x	x					
snowcover									x		
snowdepth										x	
ice_days	x		x		x						
hot_days			x								
temp_jan		x		x		x					
temp_july							x				
temp_year								x			
dem											x
land cover data (excl. prop_rocksnow)	x†	x†	x†	x†	x†	x†	x†	x†	x	x	x
water	x	x	x	x	x	x	x	x	x	x	x
established regions (A) — AUC	0.723	0.753	0.718	0.739	0.727	0.747	0.73	0.73	0.727	0.727	0.727
established regions (A) — PI (1st, 2nd)	conif# =21.7 (-) settl§ =48.9 (+)	conif# =19 (-) temp_jan =18.7 (+)	conif# =20.5 (-) settl§ =17.1 (+)	conif# =21 (-) temp_jan =18.1 (+)	conif# =20.8 (-) settl§ =18.8 (+)	settl§ =19 (+) / conif# / temp_jan =18.7 (-/+)	conif# =24.5 (-) settl§ =19.7 (+)	conif# =25.8 (-) settl§ =17.4 (+)	conif# =24.6 (-) snow cover =19.4 (-)	conif# =5.9 (-) snow depth =18.5 (-)	conif# =24.1 (-) open§ =21.9 (-)
recently invaded regions (B) — AUC	0.762	0.743	0.77	0.74	0.759	0.742	0.762	0.78	0.741	0.733	0.795
recently invaded regions (B) — PI (1st, 2nd)	ice days =76.7 (-) conif# =9.1 (+/-)	conif# =41.8 (+/-) decid¶ =21.7 (+)	hot days =41.2 (+) conif# =15.8 (+/-)	conif# =41.5 (+/-) decid¶ =22.2 (+)	ice days =76.8 (-) conif# =8.8 (+/-)	conif# =41.1 (+/-) decid¶ =20.4 (+)	temp_july =58.5 (+) conif# =25 (+/-)	temp_year =68.6 (+) conif# =20.7 (+/-)	conif# =34.6 (+/-) snow cover =23.5 (-)	conif# =38.9 (+/-) settl§ =25.1 (+)	dem =76.3 (-) conif# =11.2 (+/-)
Austria (C) — AUC	0.78	0.766	0.786	0.774	0.782	0.762	0.772	0.773	0.761	0.757	0.773
Austria (C) — PI (1st, 2nd)	ice days =34.5 (-) settl§ =27.3 (+)	temp_jan =28.9 (+) settl§ =26.8 (+)	hot days =39.1 (+) settl§ =18.3 (+)	temp_jan =30.2 (+) settl§ =25.6 (+)	ice days =36.7 (-) settl§ =28 (+)	settl§ =29 (+) temp_jan =27.8 (+)	temp_july =42.5 (+) settl§ =28.5 (+)	temp_year =50.2 (+) settl§ =23.8 (+)	snow cover =33.5 (-) settl§ =18.3 (+)	settl§ =31.6 (+) snow depth =27.7 (-)	dem =43.2 (-) conif# =16.8 (-)

Fig. 3. Changes in the probability of raccoon presence within the best performing MaxEnt model per study region (A – established regions, upper part; B – recently invaded regions, middle; C – entire state territory, lower part) depending on the two most important environmental predictors, respectively.

11-B; Table 4), representing the variable choice of the introduced-range expert. Within this model, elevation gains the highest permutation importance (PI=76.3), thus having the strongest impact in these particular models, followed by the proportion of coniferous forests (PI=11.2). Altitude has a strong negative effect on the probability of presence (Fig. 3), but in the case of the proportion of coniferous forests, the probability of raccoon presence first increases to an optimum value of 40% and thereafter decreases.

For the entire nation (C), the highest model performance (AUC 0.786) is reached by including landcover data (excluding the proportion of rocks and permanent snow cover), the water network, the sum of winter precipitation, the number of ice days, and the number of hot days per year (model 3-C) as a subset of the native-range expert's choice of variables (Table 4). The variables mainly influencing this model are the number of hot days (PI=39.1) and the proportion of settlements (PI=18.3); both are positively correlated with the probability of raccoon presence (Fig. 3).

Generally, within all tested combinations of environmental predictors a positive effect of the proportion

of settlements, the number of hot days and temperature parameters (mean temperature of the year, in summer and winter, as well as number of hot days) on the probability of raccoon presence in all regions is evident. In contrast, altitude, the number of ice days, snow depth and the duration of snow cover are negatively correlated with modeled probabilities of presence in all cases, and the same applies to the proportion of open areas in regions of established raccoon occurrences.

DISCUSSION

The raccoon's preferred landscapes in Austria

Although the number of raccoon records is relatively low in Austria (e.g. compared to Germany), particularly in regions where raccoons have recently invaded, our models performed well (AUC>0.7; [60]) showing a high PP of raccoons in Austria's cities and river valleys. These results are not surprising, as the raccoon's success has been attributed to urbanization. Raccoons thrive in urban and suburban settings alike (e.g., [(4,61]). They are so successful in human-altered landscapes that they are characterized as a "synanthropic" species, a term describing wild animals that flourish from an association with people. Furthermore, raccoons are typically most abundant near water [25,37], travelling along streams and lakes in search of food, and in other mesic habitats such as hardwood swamps, fresh and saltwater marshes, and bottomland forests. They are quite capable swimmers, a trait that could help them expand their range [4]. Consistent with these observations, our results predict a high probability of presence along the big river valleys in Austria; in particular, along the Danube there are clear hints of raccoon immigration from the northwest that is spreading into the surrounding areas, e.g. in the Muehl- and Innviertel (compare Fig. 2). Furthermore, based on our results bigger cities such as Vienna, Linz, Wels, Salzburg, and Graz, are expected to be future hotspots of raccoon occurrence.

By dividing Austria into different regions (established vs. newly invaded regions), areas with a predicted high PP persisted, but model performance partially decreased, probably due to the fact that many variables showed a lower variability within the remaining

regions. Nevertheless, modeling the PP for established and newly invaded regions allowed for a differentiation of environmental drivers of raccoon distribution in regions of different invasion status. In our study, these differences mainly considered precipitation and snow parameters, as well as the expected influence of elevation on raccoon distribution.

Climate drivers of raccoon distribution

The response curves of the included environmental variables generally showed that, besides the proportion of settlements, all temperature-linked parameters seemed to be positively correlated to the raccoon's distribution in both study regions. In those parts of Austria where raccoon populations were assumed to be established, the mean temperature in January is one of the strongest predictors of the probability of racoon presence, and for the entire state territory, the number of days with a maximum temperature of at least 30°C has the highest impact. Although raccoons are known to adapt to cold weather [4,7,38], temperature has been shown to affect raccoon distribution in Iran as well as other places [43]. Similarly, raccoon populations are expected to be higher with increasing temperatures in North America (e.g. especially in the more humid southeastern and south-central regions), but they can do well in relatively cold areas if other basic requirements of the species, such as shelter and food, are met [1,4]. To endure winter temperatures and food limitation, they accumulate fat as energy deposits [62,63] and change their spatial behavior by sharing winter dens with advantageous microclimatic conditions [41].

In those regions recently introduced by raccoons, the temperature parameters seem to play a minor role. However, altitude, as the most important predictor in these regions, is strongly linked to different climate parameters, e.g. temperature and snow cover. The combination of low winter temperatures and a close snow cover induces raccoons to stay in their winter dens and live on their fat reserves unless the snow is melting [38,64]. In the Alps, these winter conditions can last for several months and could therefore take raccoons to their limits, especially the juveniles [65]. Moreover, strong winters and high snow depths can decrease mating success due to reduced mobility [38,66]. Consequently, altitude has previously been

suggested to influence the distribution of raccoons in their introduced range [42,43]. In their native range, raccoons are also not expected to do well at high altitudes such as in the Rocky Mountains of western North America, though they occur in this region's nearby cities (and their suburbs), such as in Salt Lake City, Utah, which is 1288 m a.s.l. [1]. Thus, even at higher altitudes, human settlements are attractive for raccoons as they provide food and shelter, but they first need to get there by colonizing less suitable highland habitats or with human help (e.g. releases). Elevation obviously is a predictor of lower importance in established regions and our results reflect this as well. The regions with established raccoon populations in Austria mainly include the non-alpine regions, where altitude plays a minor role. However, running iSDMs based on climate change scenarios [67] might yield distinctly deviating predictions for raccoon distribution within the entire alpine range.

Land-cover drivers of raccoon distribution

In regard to the land-cover parameters, our results show that the proportion of coniferous forest is the most important environmental predictor of raccoons in regions of their established occurrences in Austria, with a clearly negative effect on their colonization. Some type of avoidance of coniferous forests vs. deciduous forests, as well as avoidance of open areas by raccoons has previously been shown, e.g. in the marshlands of northeastern Germany [68]. In recently invaded regions, the proportion of coniferous forests is also an important predictor. But in contrast, the PP increases until the cover of coniferous forests reaches 40% of the land cover and then strongly decreases. This effect could again be linked to altitude, as tree species compositions of forests are frequently dominated by coniferous species at higher altitudes, and forest cover, irrespective of the proportion of deciduous trees, seems to better meet the raccoon's needs compared to open landscapes. On the other hand, a low proportion of one land-cover type could indicate a more structured landscape and [12] suggests that the aggregation of woodland patches is especially important for raccoon colonization.

In contrast to established regions with large agricultural areas, spacious open areas below the timber

line in alpine regions are scarce and thus this predictor seems to be less important in recently introduced regions in the alpine areas. The raccoon's typical avoidance of treeless areas [1,7,68] is stronger in its established regions in Austria. Interestingly, the raccoon affinity for wetland habitats promotes its spread along riversides but does not seem to drive its colonization of particular areas in Austria: due to a very dense network of different water bodies with a mean of 1.2 km per square km [69], water availability does not appear to be a limiting factor for the raccoon in Austria. Probably this variable only affects raccoon activity on a local scale [25,43] and thus its impact could not be recognized with our regionally scaled data. Moreover, the high abundance of water bodies could explain the weaker influence of precipitation on raccoon distribution than expected by the experts.

The change of habitat requirements

Our results show different drivers of raccoon distribution in regions with an established population vs. those with the beginnings of colonization. As hypothesized, the environmental predictors chosen by the raccoon expert from its native range could better reflect the situation in the established regions, and the variables assumed as drivers by the expert of the introduced range led to better predictions in regions with an early stage of colonization. Thus, it can be assumed that raccoons select different habitats during the different stages of their invasion. These kinds of niche shifts during the invasion process have been shown for many alien species and were first documented by [40]

Altitude and linked temperature parameters are among the most important drivers of the raccoon's distribution in Austria. The elevation parameter especially indicates a higher degree of specialization during the early stages of colonization. Consequently, the lowlands were settled first and the largest number (78%) of records reported before 2000 is from Austria´s non-alpine regions [10]. However, there are also changes in the ecological niches of raccoons that cannot be explained by their invasion status. The avoidance of coniferous forests and of open areas was stronger in the established regions, leading to the assumption that raccoons can adapt very well to regional habitat conditions related to land cover, even in an early stage of invasion. It is likely that climate predictors overrule the importance of land-cover predictors, but this is apparently not the case for the land-cover predictor 'proportion of settlements', as human settlements represent an attractive raccoon habitat even in the climatically inhospitable alpine environment.

Uncertainty assumptions

For modeling, we did not only implement occurrence data of the categories 1 and 2 (Table 1) but also sightings by experts, i.e. persons with any kind of biological education, and sightings of dead raccoons, as we assumed the characteristics of raccoons to be easily recognizable. Due to the small sample size of categories 1 and 2, we also implemented reports of sightings by non-experts after personally contacting these individuals. We excluded obviously uncertain or implausible reports from our analyses. Nevertheless, records of lower quality represent elements of uncertainty for our results.

We did not implement literature data on raccoon occurrences in the model as these are of unknown quality. However, we used these "historical" data to distinguish regions of established raccoon populations from those recently invaded by raccoons according to the definition of [54]. Our delimitation is justified by this definition, but might hold some uncertainty, as the historical distribution range could have been underestimated or former occurrences may have disappeared. The data on reproduction of raccoons in the study area are still limited and therefore we do not know about the persistence of raccoons in the established regions for more than one generation. However, in case that a recent raccoon record was found within the historical distribution range, we assumed that raccoons have been living within that region for at least three generations and thus meet the definition of established occurrences there. After this classification of established versus newly invaded regions, we only used recent records for modeling.

Suggestions for management and modeling

As suggested previously [3], the management of raccoons – which is mandated by EU law – should concentrate on areas with optimal habitats that poten-

tially host source populations for further colonization. Based on our map of probability of raccoon presence, such focal areas for the future management of raccoons in Austria can be highlighted. These areas hold a high potential for conflicts with nature conservation targets. Such areas are mainly located in the northwest and along the northern border of the Alps, but also include the large river valleys as well as the smaller basins in the south. An upcoming problem could be the management of raccoons in the cities, where they can reach very high population densities [70], especially as hunting and trapping are forbidden in settled areas by Austrian provincial hunting laws. Consequently, it is necessary to consistently monitor the further spread of raccoons and to consider new ways of managing them in settled areas, where the transmission risk of the zoonotic raccoon roundworm (*Baylisascaris procyonis*) to humans is highest [71].

Beyond these management prospects, our results suggest a clear need to involve both climatic as well as land-cover data when predicting the future racoon distribution. Furthermore, as the habitat requirements of this flexible generalist might change, e.g. during colonization, there is a need to consider the state of the invasion in any prediction of raccoon distribution. Although iSDMs can be useful tools to predict a possible future of invasive alien species and assist in the development of management plans, they can only reflect parts of reality [72,73].

Species distribution patterns not only result from the dispersal capacities of species and their spatial distributions under favorable environmental conditions, but also from the biotic interactions between target species, competitors, predators and pathogens, which are rarely considered explicitly. As highlighted by [74], causation might not be determined by correlation, but ideas on functional relations can be approached. Therefore, the results of our model should be interpreted with caution. Nevertheless, our findings provide an understanding of the mechanisms that underlie the spread of this successful and highly adaptable invader.

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