



First assessment of habitat suitability and connectivity for the golden jackal in north-eastern Italy

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Abstract

Compared with the rapid expansion across Europe, the golden jackal colonization of Italy is still limited and slow. No study focused on the habitat selection or landscape connectivity for this species was performed in Italy; thus, the potential distribution and dispersal patterns in the country remain unknown. Our objectives were to evaluate the suitability of the Friuli-Venezia Giulia region (north-eastern Italy) for the golden jackal, as well as to identify the ecological corridors connecting the areas currently occupied by the species. Corridors modelling allowed us both to hypothesize the dispersal dynamics occurring in the study region and to identify possible obstacles to future range expansion. We surveyed golden jackal presence in two study areas, covering an area of 500 km², from March 2017 to February 2018. Using collected data, we modelled the species home-range scale habitat suitability based on an ensemble modelling approach. Subsequently, a habitat suitability prediction at a finer scale was used to estimate landscape resistance, starting from which, we modelled dispersal corridors among areas currently occupied by the species using a factorial least cost path and a cumulative resistant kernel approach. Our results indicated a moderate potential for large parts of the study region to support the occurrence of golden jackal family groups, whose presence seems to be mainly driven by the presence of wide areas covered by broadleaved forests and shrublands and by the absence of wide intensive agricultural areas. The predicted connectivity networks showed that three main permeable corridors are likely to connect golden jackal occurrence areas within the study region, while all the other corridors are characterized by a very low path density. Both the habitat selection and connectivity analyses showed a strong negative impact of the intensive cultivated plain on species stable presence and movement providing critical information for the conservation of the golden jackal in Italy.

Keywords *Canis aureus* · Dispersal flows · Ecological corridors · Habitat suitability models · Species colonization · Friuli-Venezia Giulia region

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Introduction

The golden jackal (*Canis aureus*) is a native species of the Balkan Peninsula (Kryštufek et al. 1997) and its historic distribution was mainly restricted along the Mediterranean and the Black Sea coasts (Trouwborst et al. 2015; Krofel 2018). During the last decades, the jackal not only expanded across the Balkan Peninsula but also towards north-eastern and central Europe (Kryštufek et al. 1997; Arnold et al. 2012; Trouwborst et al. 2015; Krofel et al. 2017) with dispersing individuals recorded in different countries of northern and western Europe (Hoffmann et al. 2018; Lanszki et al. 2018a and reference therein; Spassov and Acosta-Pankov 2019). In general, jackal populations are increasing in all European countries (Krofel et al. 2017). The species expansion was primarily triggered

by the decrease of the wolf (*Canis lupus*) abundance that occurred in Europe during the last 150 years (Trouwborst et al. 2015; Krofel et al. 2017). Possible additional factors include abundant and easily accessible anthropogenic food resources (Lapini et al. 2014), changes in land use and wildlife management (Markov 2012; Krofel et al. 2017), and possibly climate changes (Fabbri et al. 2014).

Thanks to the great adaptability and the opportunistic feeding habits, the species inhabits a wide variety of habitats in different climatic areas of Europe, such as Mediterranean coastal vegetation, continental mixed forests, and marshlands (Ranc et al. 2018). Moreover, golden jackals are highly adapted to live in human-modified habitats where they take advantage of a variety of anthropogenic resources (Macdonald 1979; Jaeger et al. 2007; Ćirović et al. 2016; Lanszki et al. 2018b). Given the great variability of occupied habitats, only a few factors seem to influence the jackal habitat use, i.e. the availability of food resources and the presence of vegetated areas to be used as shelter and denning (Jhala and Moehlman 2004; Borkowski et al. 2011); nevertheless, according to the available knowledge, golden jackals are mainly associated with shrub vegetation and heterogeneous agricultural landscapes (Giannatos 2004; Šálek et al. 2013).

The golden jackal is a species of community interest under the Habitats Directive (Annex V) and the member states are thus bound by the obligation to achieve a favourable conservation status for this species at the national level (European Commission 2007).

Compared with the widespread and rapid expansion observed across Europe during the last decades (Arnold et al. 2012; Trouwborst et al. 2015; Spassov and Acosta-Pankov 2019), the colonization of Italy by the golden jackal appears limited and slow. Here the presence of the species was detected for the first time in 1984 in the northern part of Veneto region (Lapini et al. 1993) and the reproduction was ascertained for the first time in 1985 in the central part of the Friuli-Venezia Giulia region (Lapini and Perco 1989); during the last 35 years, the species did not expand consistently throughout the country; family groups, in particular, remained substantially limited to the areas of the first appearance in north-eastern Italy (Lapini et al. 2018). Genetic analysis confirmed that the Italian jackals originated from Dalmatia and Slavonia simultaneously (Fabbri et al. 2014). The current distribution of the golden jackal is still irregular with few scattered family groups across north-eastern Italy, some transboundary groups (Slovenia and Austria), and some vagrant individuals observed far from the source areas in north-eastern Italy, e.g. in Lombardy and Emilia Romagna regions (Lapini 2019), and in neighbouring Switzerland (Trouwborst et al. 2015). Extinction risk can be very high at the local scale (Paoloni et al. 2014) and the dispersal process of individuals from other European countries, mainly passing from the south-eastern border of

the Friuli-Venezia Giulia region, is still relevant for the Italian population persistence (Fabbri et al. 2014; Lapini et al. 2016, 2018; Lapini 2019).

Information on the habitat selection of the golden jackal in Italy is still very scanty (Lapini et al. 2011) and, according to our knowledge, no more detailed published study is available on this specific topic. Habitat selection information is fundamental not only to increase the ecological knowledge of this species in a non-native and newly colonized country, but also to identify which environmental conditions would facilitate and/or hinder the future expansion of the species throughout northern Italy and, consequently, western Europe.

Herein we explored golden jackal habitat requirements in the Friuli-Venezia Giulia region to investigate the observed slow colonization pattern occurred in Italy from the middle 1980s until 2017. We hypothesized that golden jackal expansion would be significantly limited by the anthropic barrier represented by the main urban centres and the intensively cultivated plain, which covers the majority of the region; in addition, the dense road network located in this area would represent a severe mortality cause for dispersers, thus deeply limiting species expansion. Therefore, we predict that species settlement of new reproductive groups would be negatively affected by urban and intensively cultivated areas.

We modelled habitat suitability of the Friuli-Venezia Giulia region to identify areas with a high probability of occurrence based on an ensemble modelling approach. Moreover, we reconstructed the dispersal dynamics which might have led to the current species distribution, starting from the source area located at the south-eastern boundary with Slovenia, by developing a landscape connectivity model adopting a factorial least cost path and a cumulative resistant kernel approach. These analyses also provided useful information regarding future species expansions towards the west (Lapini et al. 2018; Lapini 2019) and can be of some interest for other European countries which will probably be colonized by the species in the near future.

Materials and methods

Study areas

This study was carried out in the Friuli-Venezia Giulia region where we surveyed two study areas covering a total area of 500 km² (Fig. 1). The Goritian Karst is located in the southeastern part of the region and includes the Karst plateau and the surrounding intensively cultivated plain; the Tagliamento Valley is a typical mountain area located in the northern part of the region in the Alps (Table 1).

The presence of the golden jackal was ascertained in both the study areas before the beginning of this research

Fig. 1 The study areas in the Friuli-Venezia Giulia region

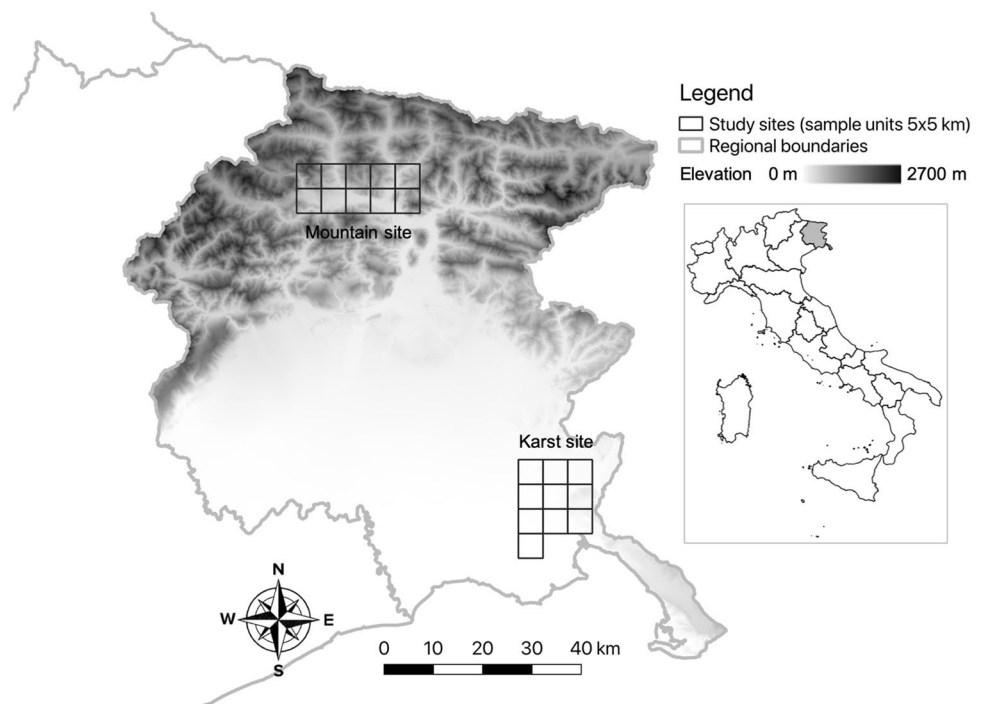


Table 1 Main characteristics of the two study areas

	Goritian Karst 13°27'37" N; 45°51'39" E	Tagliamento Valley 12°55'50" N; 46°25'27" E
Area (km ²)	250	250
Elevation (m a.s.l.)	2–225	293–1954
Land cover		
Urban areas	14.0%	3.2%
Agricultural areas		
Intensively cultivated lands% (mainly maize and soy)	46.4	
Vineyards	3.5%	
Complex cultivation patterns	8.1%	1.3%
Agricultural areas with natural vegetation	6.2%	8.8%
Forests		
Broad-leaved forests	5.6%	
Coniferous forests	2.2%	22.0%
Mixed forests	2.4%	4.5%
Meadows and pastures	0.9%	41.2%
Shrublands	7.9%	6.6%
Pebbly shore	2.0%	2.9%
Sparse vegetation		4.3%
Bare rocks		5.1%
Water bodies	0.9%	0.2%
Climate	Continental	Alpine
Mean annual temperature (°C)	13.3	10
Mean annual rainfall (mm)	1200–1800	2700–3200

(Lapini 2003, 2010; Lapini et al. 2009, 2011). In particular, species reproduction was confirmed in the Karst since the early 1990s, while it was documented more recently (around 2010) in the Tagliamento Valley (Lapini et al. 2018). Thus, both the study areas were considered important sources for golden jackal persistence in Italy (Lapini et al. 2011, 2018).

Environmental diversity of the Friuli-Venezia Giulia region sustains complex animal communities, as demonstrated by the presence of more than 90 mammal species (Lapini et al. 1996; Loy et al. 2019): considering potential golden jackal competitors, the red fox (*Vulpes vulpes*) is widespread in the whole region, whereas the wolf has a sporadic presence (Marucco et al. 2018). The Eurasian lynx (*Lynx lynx*) is present with few individuals. Considering potential prey species, wild ungulate community includes seven species with the wild boar (*Sus scrofa*), the red deer (*Cervus elaphus*), and the roe deer (*Capreolus capreolus*) being the most abundant. Among medium-sized herbivores, the brown hare (*Lepus europaeus*) is widespread; the mountain hare (*L. timidus*) and the Alpine marmot (*Marmota marmota*) are also present in the Alpine landscape; the coypu (*Myocastor coypus*) is increasing in the plain. Moreover, the region hosts a widespread community of small mammal species, i.e. *Erinaceus* sp., *Talpa europaea*, Soricidae, Gliridae, Sciuridae, Cricetidae, Muridae families.

Data collection

From March 2017 to February 2018, we monitored golden jackal presence carrying out eight monitoring sessions, i.e. four seasonal sessions in each study area (spring: March–May; summer: June–August; autumn: September–November; winter: December–February). We used three different detection techniques during each session: the collection of species signs of presence along standardized itineraries, camera-trapping, and jackal howling (Table 2).

To collect the species signs of presence, we adopted a Tessellation Stratified Sampling method (TSS; Barabesi and Franceschi 2011; Barabesi and Fattorini 2013): we divided each study area into 10 sample squares (sample units) of 25 km² (5 × 5 km) and we randomly selected three itineraries among the existing foot-paths and secondary roads within each sample unit ($n = 60$; total length = 145.1 km; min. = 1753.5 m; max. = 4006.1 m). At least three of us (ET, CD, LR) jointly walked the itineraries to record species signs of presence, corresponding to scats, footprints, and spontaneous howls. Scats were identified taking into consideration the size, shape, odour, and location (Lanszki et al. 2006; Giannatos et al. 2010; Markov and Lanszki 2012). Based on collected scats of both the golden jackal and the red fox, we assigned to the golden jackal those with a total length of 15–38 cm (mean ± SE = 21.8 ± 1.5 cm). Footprints were recorded only if part of a track: paw print shape and size, the stride and the positioning of the prints were considered

Table 2 Details on the sampling effort

		Monitoring sessions			
		Spring	Summer	Autumn	Winter
		Goritian Karst			
		March	June	September	December
Indirect signs of presence	N° surveyed itineraries	30	30	30	30
Camera-trapping	N° stations	10	10	11*	10
	Mean distance	4574.84 m	1835.33 m	1253.10 m	1330.96 m
	N° trap days	89	59	82	63
Jackal-howling	N° stations	10	10	7	7
	Mean distance	3810.04 m	2364.17 m	1694.55 m	1513.32 m
		Tagliamento Valley			
		May	August	November	February
Indirect signs of presence	N° surveyed itineraries	30	30	30	27
Camera-trapping	N° stations	8	11*	9	9
	Mean distance	3752.43 m	1356.70 m	379.16 m	565.13 m
	N° trap days	70	97	55	50
Jackal-howling	N° stations	10	5	4	2
	Mean distance	1919.29 m	5462.39 m	5013.55 m	1980.94 m

*During these monitoring sessions we deployed an additional camera trap

for species assignment (Černe et al. 2019). Scats and footprints with intermediate characteristics between similar species (i.e. the golden jackal and the red fox) were discarded; regarding the scats, we discarded those of 13–14 cm due to the overlap in their size with those of the red fox (total length range: 3–14 cm). Howls were recorded only if the typical *yiphowl* sequences were heard (Hatlauf et al. 2016). Every sign of presence was autonomously evaluated by the researchers conducting the fieldwork and discordant records were discarded.

We mounted ten camera traps ($n=8$ MULTIPIR 12 HD; $n=2$ IR-PLUS BF 110°) for a minimum period of 5 days in each site during each session (min. sampling period per study area = 50 days). Camera traps were settled mainly on trees along foot-paths approximately 0.5–2.0 m above the ground and set to record time and date when triggered. We programmed cameras to record videos (60 s) with a minimum time delay between consecutive ones (1 s) (Ancrenaz et al. 2012).

Finally, we carried out a jackal howling survey following the protocol suggested by Comazzi et al. (2016). In a single night, we emitted the playback stimuli, starting from 1 h after sunset until maximum 1 h before sunrise. Each station was possibly located in an elevated position to allow a better broadcast of the stimulus. At each howling station, we played five emissions of 30 s each. Consecutive emissions were interrupted by a 3 min silence. At the end of each session, we waited for 10 min in case of possible delayed answers by the animals. The sound intensity was increased at each emission and played towards a different direction to cover 360°.

Both camera trap and howling stations were opportunistically selected to increase the probability of detecting jackal presence; thus data collection was primarily based on the collection of species signs adopting the TSS and only secondarily was supported by opportunistic sampling to increase species detection. TSS approach, in particular, should allow a better distribution and improve the representativeness of the collected samples, as compared to, e.g., a simple random design (Barabesi and Franceschi 2011; Barabesi and Fattorini 2013).

For the analysis, we also considered the occasional direct observations of golden jackal recorded during the sampling period.

Habitat suitability analysis

To investigate the golden jackal habitat suitability, we statistically compared the environmental characteristics of locations used by the species with those of random locations (Manly et al. 2002). Specifically, a set of 333 pseudo-absence locations was randomly generated across each study site, for a total of 666 pseudo-absence locations. According

to the published literature (e.g. Šálek et al. 2013; Spassov and Acosta-Pankov 2019; Wennink et al. 2019), we calculated the percentage of 11 land cover-based variables within a circular buffer with radius of 1400 m (comparable to the smaller home-range size of a golden jackal family group; Čirović et al. 2018; Lanszki et al. 2018a) designed around each presence and pseudo-absence point to model golden jackal habitat suitability. We considered as land cover-based variables: urban areas, arable lands, permanent crops (i.e. vineyards and fruit orchards), complex cultivations (i.e. small cultivated land parcels with different cultivation types), cultivations with natural elements (i.e. areas principally occupied by agriculture interspersed with significant natural or semi-natural areas), pastures and grasslands, broad-leaved woodlands and shrublands, coniferous woodlands, mixed woodlands, wetlands, and areas without vegetation (i.e. bare rocks, beaches, and other open spaces with little or no vegetation cover). The land use cartography adopted to calculate the cover of the 11 selected land-cover types was the Corine Land Cover 2012 (EEA 2018) with a spatial resolution of 100 m.

To investigate the species habitat suitability, we developed an ensemble model at the home-range spatial scale by using the “BIOMOD2” package (Thuiller et al. 2016) in R version 3.6.1 (R Core Team 2019). Before running the model, we checked pairwise Pearson’s correlation coefficient between covariates and verified that no variable pair had a coefficient higher than 0.60 (Khosravi et al. 2018). The ensemble model was implemented using a generalized linear model (GLM), a generalized boosted model (GBM), and a maximum entropy algorithm (MaxEnt) because of their high predictive power (Bosso et al. 2018; Fois et al. 2018; Khosravi et al. 2018; Maiorano et al. 2019). For every single model, we ran three replications where 75% of the presence points was used as training set, while the remaining 25% was used as test set. The accuracy of the three distribution models was evaluated through the area under the curve (AUC) of the receiver operating characteristic (ROC; Swets 1988). To develop the ensemble prediction by integrating the output of the single distribution models, we used a weighted-averaging approach through which the distribution models were weighted according to their predictive accuracy (Thuiller et al. 2009; Rodriguez-Soto et al. 2011). The performance of the ensemble model was evaluated using the AUC of the ROC (Fernandes et al. 2019; Mohammadi et al. 2019; Scherrer et al. 2019).

Based on the output of the ensemble model, we developed an ensemble predictive map for the whole Friuli-Venezia Giulia region depicting a gradient of suitability varying from 0 to 1000.

The accuracy of the predictive map was evaluated by the Boyce index (Boyce et al. 2002) using an independent dataset of 229 occasional observations collected in the whole

Friuli-Venezia Giulia region during 2017–2018 (Lapini and Meriggi, unpublished data).

Connectivity analysis

We modeled the connectivity degree among the areas currently occupied by the golden jackal in the Friuli-Venezia Giulia region by using the universal corridor network simulator software UNICOR (Landguth et al. 2012). The input data required by UNICOR are (i) the geographic coordinates of each source location and (ii) a resistance map layer. As source locations, we used the centroids of the 2500×2500 m cells permanently occupied by the species and updated with more recent records ($n=117$) in the period 2015–2018 (Lapini et al. 2018; Lapini, unpublished data). To develop the resistance map, we generated a new ensemble predictive map for the whole Friuli-Venezia Giulia based on the output of an ensemble model developed with the same analysis procedure described above but investigating the effect on the species distribution of environmental variables calculated within a buffer of 100 m. This analysis scale change was carried out because habitat suitability models have proved to be a useful alternative to movement data to parameterize resistance maps provided that environmental variables are calculated at a finer spatial scale compared to the scale generally used to parametrize habitat suitability for a species, i.e. the home-range scale (Ziółkowska et al. 2016). In fact, dispersers and resident individuals act differently with respect to habitat selection (Mateo-Sánchez et al. 2015a; Dondina et al. 2018a). Dispersers mainly depend on the availability and use of local resources during their movements (Zeller et al. 2012), while residents usually have broadscale requirements (Mateo-Sánchez et al. 2013). To obtain a resistance map representing the permeability of the landscape to the golden jackal we converted the fine-scale suitability map by using an exponential decay function (Mateo-Sánchez et al. 2015a, b; Dondina et al. 2020). Connectivity modelling was then developed adopting a factorial least cost path (Cushman et al. 2009) and a cumulative resistant kernel approach through which we calculated the least cost dispersal Gaussian kernel around each source location up to 400 km. This threshold corresponds to the maximum distance reported for long-distance dispersals performed by golden jackals in Europe (Rutkowski et al. 2015). The least cost dispersal Gaussian kernels were then summed to produce the final corridor map (Cushman et al. 2013), where the value of each pixel corresponds to the density of the least cost paths crossing that pixel.

Results

From March 2017 to February 2018, we collected 155 data of golden jackal presence ($n=132$ within the Goritian Karst and $n=23$ within the Tagliamento Valley). These

data included 33 scats, 10 footprints, 18 vocalizations (both spontaneous and stimulated), 92 events of camera trapping, and 2 direct observations (Table 3). The collected data were not affected by spatial autocorrelation (Moran's $I=-0.009$; $P=0.999$).

Habitat suitability

Among the single species distribution models performed at the home-range spatial scale, the GLM had the lowest performance in predicting habitat suitability, while the GBM had the highest (Table 4) (further details regarding the output of the single species distribution models are reported in Table S1 and in Figures S1, S2, S3 of the Supplementary material).

In the ensemble model performed at the home-range spatial scale, the fractional cover values of arable lands, broadleaved woodlands and shrublands, and mixed woodlands were the most important variables in predicting the occurrence probability of the golden jackal (Table 5). The ensemble model showed an excellent performance in predicting golden jackal occurrence ($AUC=0.964$).

The prediction resulted from the ensemble model run at the home-range spatial scale revealed that 12.2% of the whole Friuli-Venezia Giulia region had the potential to support the stable presence of the golden jackal (occurrence probability higher than 0.5). The prediction map showed that the most suitable areas for the golden jackal were located along the Karst area, in the southeastern of the region, the Julian and Carnic Prealps, which cross the border between the Alps in the north and the plain in the south, the main Alpine valleys, and the main floodplains at the plain margin (e.g. Torre, Isonzo, Tagliamento and Meduna rivers). Conversely, the most unsuitable areas for the species were located in the intensively cultivated plain and at the higher elevations in the Alps (Fig. 2).

Boyce index result suggested that the obtained prediction map was highly robust (Spearman rank correlation coefficient = 0.95), thus able to predict golden jackal presence (Fig. 3).

Connectivity

The ensemble model performed at the fine spatial scale showed an excellent performance in predicting golden jackal occurrence ($AUC=0.919$). Details regarding the output of both the single species distribution models and the ensemble model performed at the fine spatial scale are reported in the Supplementary material (Tables S2, S3, S4 and Figures S4, S5, S6, S7).

The map of the corridors produced by the factorial least cost path model performed on the resistance surface obtained from the predicted suitability map based on the output of the

Table 3 Details on the collected data

	Monitoring sessions			
	Spring	Summer	Autumn	Winter
	Goritian Karst			
	March	June	September	December
Scats	15	5	3	6
Footprints			7	1
Spontaneous howls	3	2		1
Camera-trapping events		9	53	17
Max. n° of individuals		1	3	3
Stimulated howls	1	2	4	2
N° estimated groups	1	3	2	*
Direct observations			1	
Max. n° of individuals			1	
	Tagliamento Valley			
	May	August	November	February
Scats		3		1
Footprints			2	
Spontaneous howls	1			
Camera-trapping events		3	3	7
Max. n° of individuals		1	1	2
Stimulated howls	1	1		
N° estimated groups	1	1		
Direct observations			1	
Max. n° of individuals			5	

*Only single individuals

Table 4 Accuracy evaluation of the species distribution models performed at the home-range spatial scale measured through the AUC (area under the curve of the receiver-operating characteristic)

Species distribution model	Replication	AUC
GLM	1	0.885
	2	0.930
	3	0.898
	Full	0.910
GBM	1	0.989
	2	0.989
	3	0.966
	Full	0.992
MaxEnt	1	0.887
	2	0.937
	3	0.894
	Full	0.913

Table 5 Mean score of three replications assigned to the environmental variables used to develop the ensemble model at the home-range spatial scale

Environmental variable	Variable score
Urban areas	0.006
Arable lands	0.180
Permanent crops	0.004
Complex cultivations	0.005
Cultivations with natural elements	0.032
Pastures and grasslands	0.026
Broadleaved woodlands and shrublands	0.246
Mixed woodlands	0.136
Coniferous woodlands	0.022
Wetlands	0.045
Areas without vegetation	0.035

ensemble model performed at the fine spatial scale showed a gradient of path density among the 117 source locations permanently occupied by the species in the Friuli-Venezia

Giulia region in the period 2015–2018 (Fig. 4). The prediction map showed that three most suitable corridors connect the Italian golden jackal source area located in the south-eastern Karst area to the other areas of species occurrence in

Fig. 2 Predicted suitability for the golden jackal across the Friuli-Venezia Giulia region based on the result of the ensemble model implemented at the home-range spatial scale

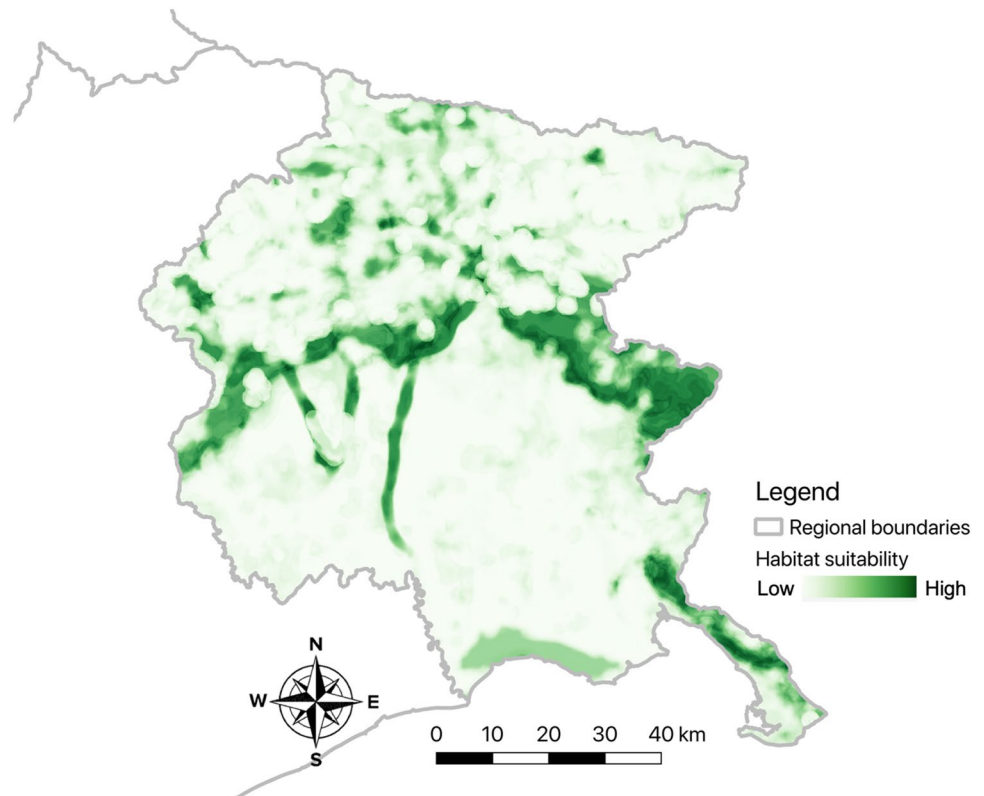
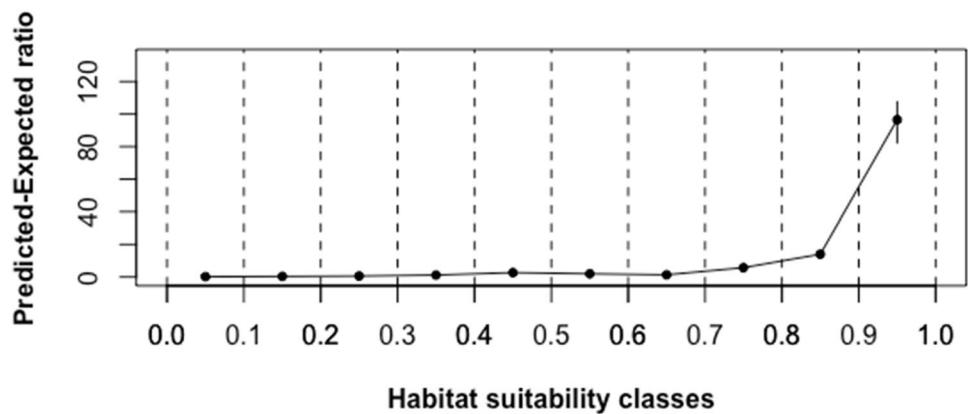


Fig. 3 Boyce index validation of the predictive suitability map for the golden jackal in the Friuli-Venezia Giulia region



the study region. The corridor characterized by the highest probability of species passage runs in the eastern part of the region and connects the south-eastern Karst area to the Julian and Carnic Prealps. A second important corridor runs on the eastern part of the region crossing the intensively cultivated plain and connects the south-eastern Karst area to the westernmost Prealpine area permanently occupied by the species. The third notable corridor horizontally crosses the western Prealps connecting the westernmost Prealpine area occupied by the species to the nucleus located in the central part of the study region Prealps. Apart from these three significant paths, several low permeable corridors connect the south-eastern Karst area to the golden jackal family groups

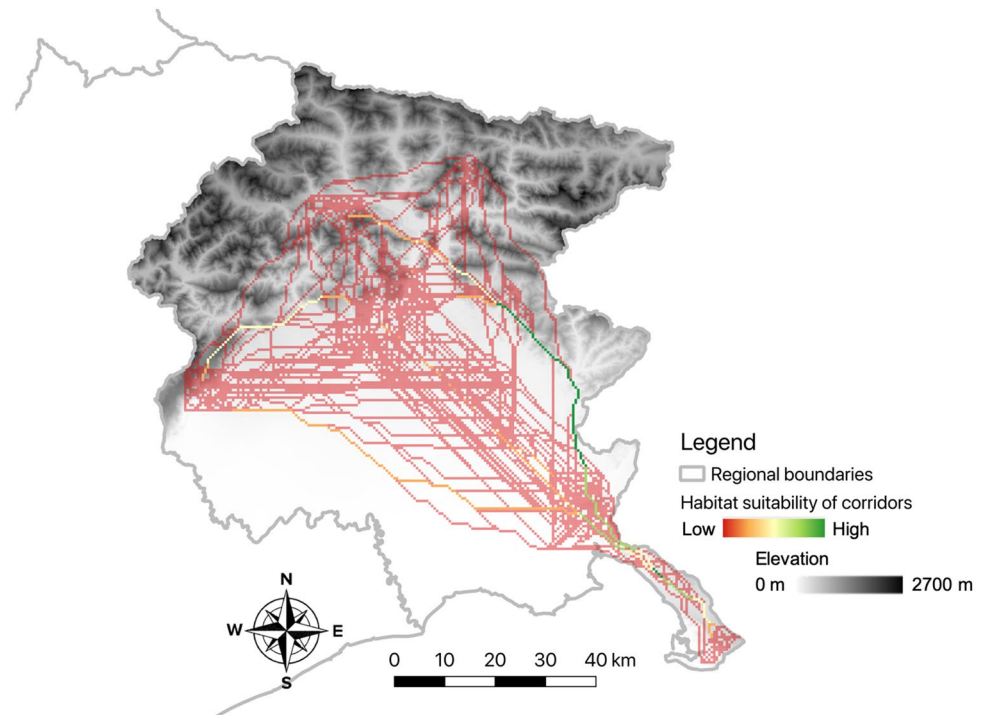
scattered in the cultivated plain and in the central part of the study region along Prealps and Alpine valleys.

Discussion

In this study, we provided the first assessment of habitat suitability and ecological connectivity for the golden jackal in north-eastern Italy, one of the key areas for species expansion towards western Europe.

Based on the ensemble habitat suitability model, wide areas of the Friuli-Venezia Giulia region were predicted as less suitable for the species. Specifically, the intensively

Fig. 4 Corridors connecting the areas permanently occupied by the golden jackal in the Friuli-Venezia Giulia region in the time period 2015–2018 developed from a resistance surface obtained from the ensemble model performed at the fine-spatial scale



cultivated plain was predicted as unfavourable to species occurrence. The main suitable areas, potentially able to support reproductive groups, were located in the Karst in the south-eastern part of the region, along the Julian and Carnic Prealps, within main Alpine valleys, and along the main floodplains at plain margins.

The cover of broadleaved woodlands and shrublands was the most important explanatory variable out of those tested in predicting the occurrence of the golden jackal in the study region; golden jackal occurrence probability increased with an increasing cover of broadleaved woodlands and shrublands. Other important explanatory variables were the cover of arable lands and mixed woodlands, with an interestingly negative effect on the probability of occurrence of the species.

Even though the golden jackal was described as a species highly capable of exploiting anthropogenic resources and agricultural landscapes (Raichev et al. 2013; Ćirović et al. 2016; Shahnaseri et al. 2019), our data showed that the key factor positively affecting species occurrence were natural habitats. Dense broadleaved vegetation, in particular, emerged as an important habitat, providing adequate resources, such as prey and den sites, as well as an adequate cover offering shelter from human persecution (Giannatos 2004).

As highlighted by Šálek et al. (2013), the intensity of agricultural management had a deep influence on golden jackal occurrence in human-dominated landscapes; in particular the increasing proportion of arable lands in a landscape negatively influenced species occurrence

probability. Conversely, heterogeneous agricultural lands (e.g. extensively agricultural areas or cultivations with natural elements), which are structurally highly diverse, provide a suitable environment for many small mammal species (e.g. Alain et al. 2006), i.e. an important potential prey for the golden jackal (Lanszki et al. 2006, 2009, 2010; Jaeger et al. 2007; Hayward et al. 2017). Accordingly, the intensive agricultural lands predominant in the plain area of our study region, which are characterized by mono-specific fields of cereals and legumes that lead to a structurally highly uniform landscape, unlikely provide adequate resources for the golden jackal, especially during the winter when soils are completely bare or covered with little vegetation thus scarcely able to support young dispersers.

As highlighted by Jenks et al. (2015), the use of agricultural landscapes probably represents a trade-off for the golden jackal, between the access to anthropogenic resources, which are concentrated and predictable, and the increased risk of mortality (e.g. human persecution or vehicle collisions). In our study region, jackals can successfully avoid arable lands because of their current low population density which implies low intra-specific competition allowing the few reproductive groups to choose the most suitable habitat types, such as broadleaved woodlands and shrublands. These habitats offer shelter, suitable areas for reproduction and abundant potential prey, from small mammals to wild ungulates, as well as wild fruits, a seasonally important accessory food category for the species (Radović and Kovačić 2010; Markov and Lanszki 2012).

The negative influence of mixed woodlands may be related to the landscape: this kind of woodland, mainly represented by beech (*Fagus sylvatica*) and spruce (*Picea abies*) or silver fir (*Abies alba*), is present at higher elevations in the Alps. In mountainous areas a few factors seem to limit golden jackal stable presence: Spassov and Acosta-Pankov (2019) stated that jackals prefer lowlands with moderate slopes and avoid mountainous regions with steep terrain, deep snow and covered by dense forest vegetation; moreover, with the increase of elevation it is expected a decrease of specific richness and diversity of small mammals (e.g. Milana et al. 2019), important potential prey for jackals.

We are quite confident that the results regarding the areas predicted as potentially suitable for the species are highly plausible because the main external factor generally influencing the distribution of the species in a specific territory, i.e. the distribution of the wolf (Krofel et al. 2017), does not act in our study region as the large carnivore is stably present only with one pack (Marucco et al. 2018).

Nevertheless in light of the above-mentioned researches regarding the golden jackal presence in human-dominated landscapes and based on the fact that in the near future wolf population will likely expand in north-eastern Italy and that this species will probably occupy firstly the more natural areas, it is plausible that the golden jackal will be forced closer to human settlements and into more cultivated habitats. Indeed the jackal is considered more adapted to exist in human-modified landscapes compared to the wolf (Krofel et al. 2017). Thus the expected changes in the wolf population might potentially impact the course of jackal colonization towards western regions.

The connectivity analysis allowed us to develop a hypothesis concerning the probable dynamics of colonization of the Friuli-Venezia Giulia region starting from the south-eastern Karst source area. Based on obtained results, it is possible to hypothesize that passing from the most suitable eastern corridor, jackals coming from the south-eastern Karst area probably reached the central areas of the study region along the Prealps and the Alps, where animals successfully settled originating the Alpine and Prealpine jackal family groups. Moreover, starting from both the south-eastern Karst area and the central Prealps, individuals reached the westernmost Prealps passing from the central Prealps and the south-western plain suitable corridors, respectively. The presence of these three highly permeable corridors connecting the source area to the central Alpine and Prealpine areas and to the western Prealps have probably allowed the presence of the family groups occupying these areas. Such permeable corridors, in fact, probably guarantee a continuous exchange of individuals over time, also after the first events of dispersal and colonization, continuously supplying the originated groups. The colonization of the few Alpine valleys suitable for the species probably occurred through one of

the numerous corridors departing from the central Prealpine area. These corridors were characterized by a low path density because this area is widely covered by permeable habitats for jackals and there are no obligatory passages in which many least cost paths converged. The more isolated golden jackal family groups scattered in the central and eastern plain could also have been originated from single occasional dispersal events of small jackal groups (Rutkowski et al. 2015) coming from both the Karst source area and the central Prealpine area and passing from one of the several corridors crossing the plain. Contrary to the Alpine situation, these corridors were characterized by a very low path density, because the plain is completely covered by impermeable habitats for jackals and no suitable habitat elements concentrate high numbers of least cost paths generating highly permeable corridors.

The described hypothesis concerning the probable dynamics of colonization of the Friuli-Venezia Giulia region is based on an ecological model and should be supported by genetic evidence currently lacking; this issue could be adequately assessed in future researches as reliable individual genotype identifications from DNA extracted from non-invasive samples might be feasible for the Italian subpopulation (see Fabbri et al. 2014).

Given the long-distance dispersal capabilities of the species (Rutkowski et al. 2015; Lanszki et al. 2018a), it has to be taken into consideration even the possibility that the occupied areas along the Prealps and the Alps and in the central and eastern plain of our study region were colonized by dispersers from other countries, e.g. from Slovenia. It is probable a continuous flow of individuals between the two neighbouring countries given the fact that jackals from Italy, Slovenia, and Austria have mixed origins from Dalmatia and Slavonia (Kusza et al. 2018).

These results suggest that the barely suitable intensively cultivated plain might limit golden jackal movements and might represent the main cause for species slow expansion toward the west. The Friuli-Venezia Giulia plain is also crossed by several traffic roads, which could significantly impact the species ability to disperse. This hypothesis is confirmed by fact that every year several dispersers die for vehicle collisions in the plain ($n=23$ from 2018 to 2020; Lapini unpublished data), making road kills the most urgent risk factor for the golden jackal in Italy, where the estimated population is about 30–50 individuals (Lapini et al. 2018).

The results of this study provide important information useful for the conservation of the golden jackal in Italy. Conservation measures for medium-sized carnivores typically require the protection of both suitable areas, potentially hosting reproductive groups, and movement corridors among them (e.g. Khosravi et al. 2018). In human-dominated landscapes, where habitat fragmentation increases species vulnerability, this issue deserves even more attention. In fact,

any loss of these habitats or corridors might result in local extinctions and in a general population decrease. Accordingly, golden jackal conservation in Italy should focus on both conserving natural areas, such as woodlands and shrublands, and by making intensively cultivated areas more heterogeneous to originate alternative permeable corridors to strengthen the effectiveness of the existing ecological network and to create new colonization routes (McRae et al. 2008; Dondina et al. 2018b).

Our results can also be interesting for other European countries where the presence of the golden jackal will be likely in the near future or it has been ascertained with only the sporadic presence of dispersers (e.g. Germany, France, Switzerland).

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Compliance with ethical standards

Conflict of interest The authors declare that they had no conflict of interest.

Ethical approval This manuscript has been approved by all co-authors.

Research involving human participants and/or animals The research complies with the guidelines or rules for animal care and use for scientific research.

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