

# Reclaiming the man-made plain: ecological factors influencing the colonization of the wolf *Canis lupus* in the western Po Plain (NW Italy)

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A - Research concept and design, B - Collection and/or assembly of data, C - Data analysis and interpretation, D - Writing the article, E - Critical revision of the article, F - Final approval of the article

## Abstract:

The wolf *Canis lupus* is recolonizing the Po plain with variable intensity and patterns depending on the areas; in the province of Lodi, colonization by wolves seems to occur very quickly due to the proximity of the Trebbia and Nure valleys, whose wolf packs fuel the species dispersal. Between 2019 to 2024, we collected 109 observations for a total of 183 wolves, which settled in the central-southern part of the province, selecting the hilly areas and the banks of the Po, Adda and Lambro rivers. Intensive monitoring has provided useful data to estimate some population parameters; the average litter size was 4.8 pups and the pack size was 8-9 wolves, data in agreement with literature information, while the average density, 0.9 ind./km<sup>2</sup> (range = 0.73-1.09), was lower than that of several European protected populations and close to the densities of culled ones. Roads, urban areas and meadows have a negative influence on the predator presence, which is favoured by green areas close to urban settlements and, though not significantly, by wetlands. On the other hand, a stable presence is favoured both by tree cover surrounded by extensive crops and by the presence of wetlands and water basins, which can provide prey such as the coypu and perhaps make access to dens more difficult, thus reducing disturbance during reproduction. The road network has a negative effect on the presence/absence pattern of the wolf, but not on the stability of its settlement, despite the high mortality rate from vehicle collisions which can remove up to 75% of the annual litter produced by some pairs. The low density observed so far makes a population increase likely in the next few years, but the speed of recolonisation throughout the territory may slowed down by the high mortality rate that hinders post-reproductive dispersal.

**Keywords:** modelling, habitat suitability, settlement, wolf, dispersal, Po plain.

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Factors influencing the colonization of the wolf in Po plain

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# Reclaiming the man-made plain: ecological factors influencing the colonization of the wolf *Canis lupus* in the western Po plain (NW Italy)

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**Key words:** *Canis lupus*, dispersal, settlement, Po plain (Province of Lodi), habitat suitability, modelling.

## Abstract

The wolf (*Canis lupus*) is recolonizing the Po plain with varying intensity. In Lodi province the process is fast, due to its proximity to the Trebbia and Nure valleys, which host dispersing populations. Between 2019 and 2024, 109 observations recorded 183 wolves settling in central-southern Lodi, favoring hilly areas and riverbanks (Po, Adda, Lambro). Intensive monitoring has provided useful data to estimate some population parameters; the average litter size was 4.8 pups and the pack size was 8-9 wolves, data in agreement with literature information, while the average density, 0.9 ind./km<sup>2</sup> (range = 0.73-1.09), was lower than that of several European protected populations and close to the densities of culled ones. Environmental characteristics where the wolf is permanently or irregularly present, or absent, are different. Roads, urban areas and meadows have a negative influence on presence, which is favoured by green areas close to urban settlements and, though not significantly, by wetlands. Stable presences are favoured both by tree cover surrounded by extensive crops, from which the wolf can better control potential threats surrounding shelters, and by the presence of wetlands and water basins, which can provide prey such as the coypu and perhaps make access to dens more difficult, thus reducing disturbance during reproduction. The road network has a negative effect on the presence/absence pattern of the wolf, but not on the stability of its settlement, despite the high mortality rate from vehicle collisions

which can remove up to 75% of the annual litter produced by some pairs. The low density observed so far makes a population increase likely in the next few years, but the speed of recolonisation throughout the territory may be slowed down by the high mortality rate that hinders post-reproductive dispersal.

## Introduction

The expansion of the wolf in a large part of its historical range in the western Palearctic has been described in detail (Chapron *et al.* 2014, Boitani *et al.* 2022). During its territorial expansion, the wolf has confirmed a strong environmental and behavioral adaptability (Zlatanova *et al.* 2014), moving into highly anthropized and urbanised habitats where it had been absent for several centuries (Herzog 2018, Boitani *et al.* 2022, Zanni *et al.* 2023, De Feudis *et al.* 2025, Meggiorini *et al.* 2024).

In the western Po Valley, the expansion and dispersal of the wolf from high density mountain areas towards lower density ones such as the underlying plain (Meriggi *et al.*, 2020) is a consequence of the demographic increase of the neighbouring Apennine populations (Torretta *et al.*, 2024). In moving from the Apennines to the plains, the species experienced a radical change in habitat, diet and social relationships; it also entered a habitat heavily populated by humans, pets, livestock with a dense network of roads, motorways, channels and urban areas (Meriggi *et al.*, 2020, Torretta *et al.* 2024). Researchers now have solid evidence that, despite the huge differences between native and colonised ecosystems, wolves can adapt quickly to new habitats (Mech, 2017), in particular by changing their diet, adapting to the few semi-natural vegetation remnants and reconstituting social groups after the dispersal phase. (Kojola *et al.* 2006; Jędrzejewski *et al.*, 2004, 2008; Nakamura *et al.* 2021).

The Province of Lodi is a small area in the Lombardy region, extending from the Po River to the outskirts of the Milan metropolitan area (Roy 2002); the rivers Po to the south, Lambro to the west and Adda to the east mark its natural boundaries, while the territory gradually meets the urbanised metropolitan matrix to the north. Although the territory is densely populated and developed, it is an important dispersal corridor for

the wolf, as it is in front of the Apennine valleys (Trebbia and Nure valleys), which host numerous reproductive packs of this predator (Meriggi *et al.* 2015, Torretta *et al.* 2024).

In the Province of Lodi, the wolf became locally extinct in 1765, as evidenced by the last recorded report of a rabid female that was killed in Orio Litta, after attacking about 16 people (Archives Ospedale Maggiore of Milan). This report, however, already exhibited the characteristics of an exceptional event and concerned an isolated and ill individual (Comincini 1991). It is highly probable that the wolf, as a native species capable of stable reproduction, had become extinct at least a century earlier.

Since 2019, the wolf has been observed with an unusual frequency in the Lodi plain, where it has settled and reproduced since the first year of its presence, quickly establishing several packs and expanding rapidly northwards. Understanding the habitat and trophic characteristics that allowed the wolf to rapidly establish stable packs capable of feeding the species' expansion northwards is important in order to i) provide useful information to improve management of a large predator in densely populated areas, ii) understand how and whether lowland areas can support viable wolf populations, iii) understand if the ecological corridors in the Po Valley are able to guarantee the connectivity between the Apennine and Alpine wolf populations, in addition to those along the Ligurian Apennines.

The aim of this study was to describe the dynamics of wolf expansion in the province of Lodi and to identify the environmental characteristics that allow the recolonization process. In particular, we analysed the dynamics of the presence of the wolf in the municipalities of the province of Lodi (Lombardy) from 2019 to 2023 and we related the stable presence to the environmental characteristics. Our main hypothesis is that the wolf is favoured by the extension of the woods along the rivers and disadvantaged by the anthropization of the region. We used municipalities as spatial units to be able to trace the probability of stable wolf presence back to easily identifiable administrative borders, so that in the future it will be easy to adopt appropriate actions to raise public awareness and prevent any damage.

## Study area and methods

### *Study area and environmental variables*

The study area coincides with the province of Lodi located in southern Lombardy (45°28'01.25'' - 45°03'08.14'' N; 9°18'26.23'' - 9°52'49.41'' E; Figure 1); the population density is 293 inhabitants/km<sup>2</sup>, which has been increasing rapidly over the last thirty years. The area is highly urbanized in the northern part bordering the metropolis of Milan while population density is lower in the southern part along the Po River. However, these areas are undergoing a rapid urban transformation due to the expansion of local industries and freight depots. The Po, Adda and Lambro rivers mark the southern, eastern and western borders of the area that belongs to the Padana sedimentary basin. The study area is characterized by a slight slope towards the south and a general morphological uniformity, except for the secondary water network, which extends for about 2300 km across the province. The environment of the Province of Lodi is characterized by large agricultural areas, mainly cereal crops, dominated by short rotation intensive crops (maize and related annual crops), which cover 74.3% of the surface. Anthropized areas account for 13.1%, including urban areas (6.2%), industrial areas (4.7%) and infrastructures (2.1%); forests are a third important habitat variable (3.8%). Other habitat variables, such as cultivated woodland and scrubland, together with roads and infrastructures, are each around 2% of the total area, while water basins, oxbows and associated natural vegetation are less important and fall below 1% (Table I).

The climate is continental with hot, muggy summers ( $T_{\max} = 29.7^{\circ}\text{C}$ ) and cold winters (mean  $T = -0.8^{\circ}\text{C}$ ). Average precipitation amounts to 843 mm/year and is concentrated in spring and autumn.

The province of Lodi is an agricultural and husbandry area: in 2023 the livestock sector consisted of about 200,000 cattle, 400,000 pigs and 600,000 poultry (Coldiretti

archives). This considerable supply of potential prey is essentially worthless to the wolf, since it is farmed under controlled conditions and in enclosed spaces. In recent years there has been a slight increase in the number of cattle reared outdoors, and a certain amount of prey is available during the temporary passage of sheep that settle in the lowlands during the winter. Wild ungulates such as roe deer *Capreoleus capreoleus* and wild boar *Sus scropha* are found only in a few protected areas but at low densities.

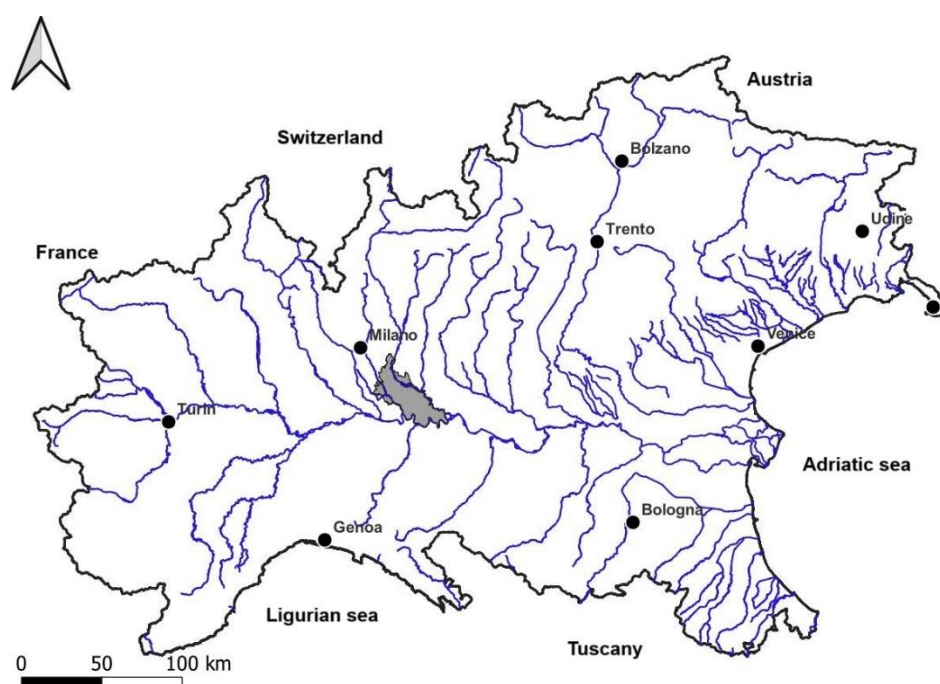


Figure 1. Location of the province of Lodi in Northern Italy (in grey). The main towns and rivers are evidenced.

### Data collection

We collected information about wolf presence either opportunistically or as a result of ad hoc research carried out in the province of Lodi, along the territorial borders or in municipalities that historically belonged to the province (e. g. hilly area of San Colombano al Lambro MI). The data collected included different types of observation and different sources. Observation of an individual was considered an index of presence, and observation of cubs with one or more adults was considered evidence of reproduction. Reproduction was only accepted as valid evidence if the litter behaviour



showed dependence on parental care (i.e. feeding by adults); the observation of litters observed only once was not considered sufficient evidence of in situ reproduction, whereas repeated observations in the same areas, in the presence or absence of adults, were considered evidence of in situ or nearby reproduction. So, litters were identified by number of cubs, their estimated age and the pack size. To support this approach, this type of observation was verified and validated where independent juveniles had been filmed in previous years. Opportunistic data were collected by several observers and subsequently accepted or rejected following SCALP criteria (see below); data from ad hoc research are the outcomes of master thesis carried out in some protected areas of the Province of Lodi (i.e. SIC/ZPS IT2090001 Monticchie and SIC IT2090010 Adda Morta).

We classified the observations according to the SCALP criteria (Molinari-Jobin *et al.*, 2012; La Morgia *et al.*, 2022). Category 1 (C1) = certain evidence from observations of live or dead individuals, georeferenced photographs and videos, genetic records; Category 2 (C2) = observation confirmed by experts as scats, predation upon wild or domestic animal, spontaneous or induced howls, direct observations without supporting documentation; Category 3 (C3) = any other type of report or testimony or unconfirmed data (e.g. sightings not confirmed by an expert).

Since C3 observations must be considered with caution as they can include both false presence and wrong identification, all C3 reports were validated only if they refer to at least 3 data collected by at least 2 observers in the same area; moreover, all observations of tracks and footprints were excluded from analysis. This selection eliminated 29 observations not fully reliable and a total of 109 observations were confirmed between 2019 and 2024.

Then we classified the municipalities by the presence or absence of the wolf in each year and calculated the frequency of wolf sightings and the number of wolves for each observation. We also classified the municipalities as municipalities with wolf presence (at least one year of presence) and absence (absence in all years); furthermore, we

classified the municipalities as having stable wolf presence ( $\geq 3$  years of occupancy) or sporadic presence ( $< 3$  years of presence).

### *Habitat variables*

We analysed a total of 28 environmental variables for the 63 municipality in the study area. We used the software QGIS v. 3.22.2 and the regional land use map (DUSAF [https://www.geoportale.regione.lombardia.it/news/-asset\\_publisher/80SRILUddraK/content/dusaf-7.0-uso-e-copertura-del-suolo-2023](https://www.geoportale.regione.lombardia.it/news/-asset_publisher/80SRILUddraK/content/dusaf-7.0-uso-e-copertura-del-suolo-2023)) to calculate the environmental variables for each municipality.

Main variables were: urban areas including hamlets, farmhouse, urban surface, factories; infrastructures including highways and railways; agricultural environment including horticulture, garden, orchards, rice fields, meadows, and cereal crops; woodland areas including poplar groves, mixed natural woodland, riparian vegetation, and shrubland; natural habitat including the course of rivers, their beds along with the riverbeds, oxbows, water basins and channels; Protected Areas i.e. Nature Reserve and SCI. Environmental metrics of the study area are in Appendix A and B.

### *Data analysis*

We tested for statistical differences of the 28 variables between municipalities with the species in at least one year and without in all years by the Student t-test; furthermore we carried out the same analysis by pooling occupancy data from 2019 to 2024 and considering the stable ( $\geq 3$  years) and sporadic ( $< 3$  years) presence of the wolf over the whole study period. To identify which variables influenced the wolf presence in the municipalities of the study area, we formulated two GLM models (family Binomial, function Logit) with the environmental variables as predictors, the first to forecast the simple presence of wolves with as dependent variable the presence in at least one year of the study period (1) and the absence throughout the period (0) and the second to predict the probability of stable wolf occurrence, with as dependent variable the stable



presence (1) and absence or sporadic presence (0) in the municipalities. Variable selection was made by the stepwise forward procedure and the Akaike Information Criterion corrected for small samples (AICc, Akaike 1973; Anderson *et al.* 2000, 2001; Burnham and Anderson 2002) and the significance of coefficients was tested by the Wald statistic. We evaluated the model performance by the difference of the AICc with that of the null model ( $\Delta AICc$ ), by the explained deviance ( $D^2$ ; Yee e Mitchell, 1991; Boyce *et al.*, 2002; Zuur *et al.*, 2007, 2009, 2010) and by the area under the Receiver Operating Characteristics (ROC) curve (AUC), which can assume values ranging from 0.50 (random prediction of the model) to 1.00 (perfect prediction of the model). Model discrimination ability was categorized as excellent for  $AUC > 0.90$ , good for  $0.80 < AUC < 0.90$ , acceptable for  $0.70 < AUC < 0.80$ , bad for  $0.60 < AUC < 0.70$  and null for  $0.50 < AUC < 0.60$  (Swets, 1988). Finally, we computed the Variance Inflation Factor (VIF) with a threshold of 3 to test for variable collinearity, and the Q-Q plot to check for residual normality (Quinn and Keough 2002, Zuur *et al.* 2010). We performed statistical analyses with the software R 4.4.3 and the package R Commander (Fox *et al.* 2024).

## Results

### *Temporal dynamics of recolonization.*

The colonization of Lodi province by wolves started in 2019 when we recorded the species presence in four municipalities covering in total 74.1 km<sup>2</sup>. In the following years, the presence of the wolf spread, arriving in 2023 to progressively occupy 253.8 km<sup>2</sup> and 18 municipalities. In 2024, we recorded a slight contraction of the wolf range with 14 municipalities occupied for a total of 223.0 km<sup>2</sup> (Figure 2); at the end of the study period in 2024, wolves were recorded on 27.1% of the study area.

From 2019 to the end of 2024, we collected in the province 109 reports of wolves, representing 168 observations (Appendix C). The data include direct observations of

individuals (84.7%) and predations (7.7%), while vehicle collisions and signs of presence accounted for 6.0% and 1.6% respectively. Over the observation period, the average number of individuals per observation ( $\pm$  SE) was  $1.7 \pm 1.25$  (1-9), ranging from a maximum of  $2.3 \pm 2.5$  in 2019 to a minimum of  $1.3 \pm 0.6$  in 2020, while the total number of individuals recorded reached a maximum of 57 and 62 in 2021 and 2023, respectively; during the study period the average wolf density in the study area was  $0.89 \text{ ind/km}^2$  (range =  $0.73\text{-}1.09 \text{ ind/km}^2$ ).

Reproductions of the species have been repeated over the years and breeding pairs and small packs have become permanently established in some of the first areas of settlement, all of which were located near protected areas and nature reserves along the river Adda. A first breeding was reported in 2019 along one of the natural channels near the river Adda, but it did not recur. No breeding was confirmed in 2020, but in 2021 a pair bred along the main course of Adda river. From 2022 onwards, at least 4 reproductions were yearly reported in four the municipalities (Figure 2); a possible reproduction was also reported along the course of the river Adda north of Lodi, but it was not possible to verify it. Litters averaged ( $\pm$  SE)  $4.8 \pm 2.1$  pups and annual averages varied from a minimum of  $3.7 \pm 0.5$  in 2022 to a maximum of  $6.3 \pm 2.5$  the following year. The repetition of reproductive events favoured the constitution of at least three wolf packs in the territories of three municipalities, one of which was formed by as many as 9 individuals in 2022 and 8 in 2024. All packs remained together until late summer each year, and in some cases until late December, after which they diminished rapidly, probably following the dispersal of the young. In a single case a young female remained in contact with the adult pair until breeding the following year.

In the case of the largest pack of wolves, mortality from vehicle collisions was high. Many pups died during the autumn-winter dispersal period: of a total of 63 observations of pups recorded between 2021 and 2024, 8 died from vehicle collisions before winter and 7 of these from the “Monticchie” Nature Reserve area, where the largest group of wolves is present. Here, mortality per cohort ranged from 50% in 2022-

23 to 75% in 2024; in some areas, mortality from vehicle strikes may therefore wipe out the net productivity of local wolf populations.

### *Habitat features influencing recolonization*

Municipalities with the presence of wolves in at least one year of the study period were different from those in which the wolf was never present for seven environmental variables (Table I). In particular, urban areas and meadows were more represented where the presence of the wolf has never been recorded, while arable land, poplar groves, bushland, watercourses and water basins had higher percentages in the municipalities where the wolf was present.

Between municipalities with stable occupancy by wolves and sporadic or absence ones, significant differences resulted only for deciduous woods, water basins, and nature reserves; all these variables had higher percentage values in the municipalities with a stable wolf presence (Table II).

Table I Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf presence (N = 28) and absence ones (N = 35) (Student t-test).

Variables	Presence	Absence	t	P
Poplars	3.5 (0.74)	1.5 (0.22)	2.87	0.006
Meadows	7.1 (1.35)	10.8 (1.31)	1.99	0.051
Scrubland	2.0 (0.27)	1.1 (0.16)	2.96	0.004
Watercourses	2.5 (0.49)	1.3 (0.24)	1.30	0.018

Table II Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf stable (N = 14) and sporadic (N = 49) presence (Student t-test).

Variables	Stable presence	Sporadic presence	t	P
Arable lands	82.1 (1.72)	62.8 (1.39)	2.05	0.044
Poplars	3.8 (1.17)	2.0 (0.33)	2.08	0.042
Tree crops	1.5 (1.22)	0.1 (0.03)	2.16	0.035
Deciduous woods	2.2 (0.87)	0.9 (0.24)	2.20	0.032
Riparian woods	4.9 (2.05)	2.5 (0.22)	2.10	0.040
Wetlands	0.4 (0.18)	0.1 (0.03)	3.03	0.004
Nature reserve	3.8 (3.13)	0 (0)	2.34	0.023

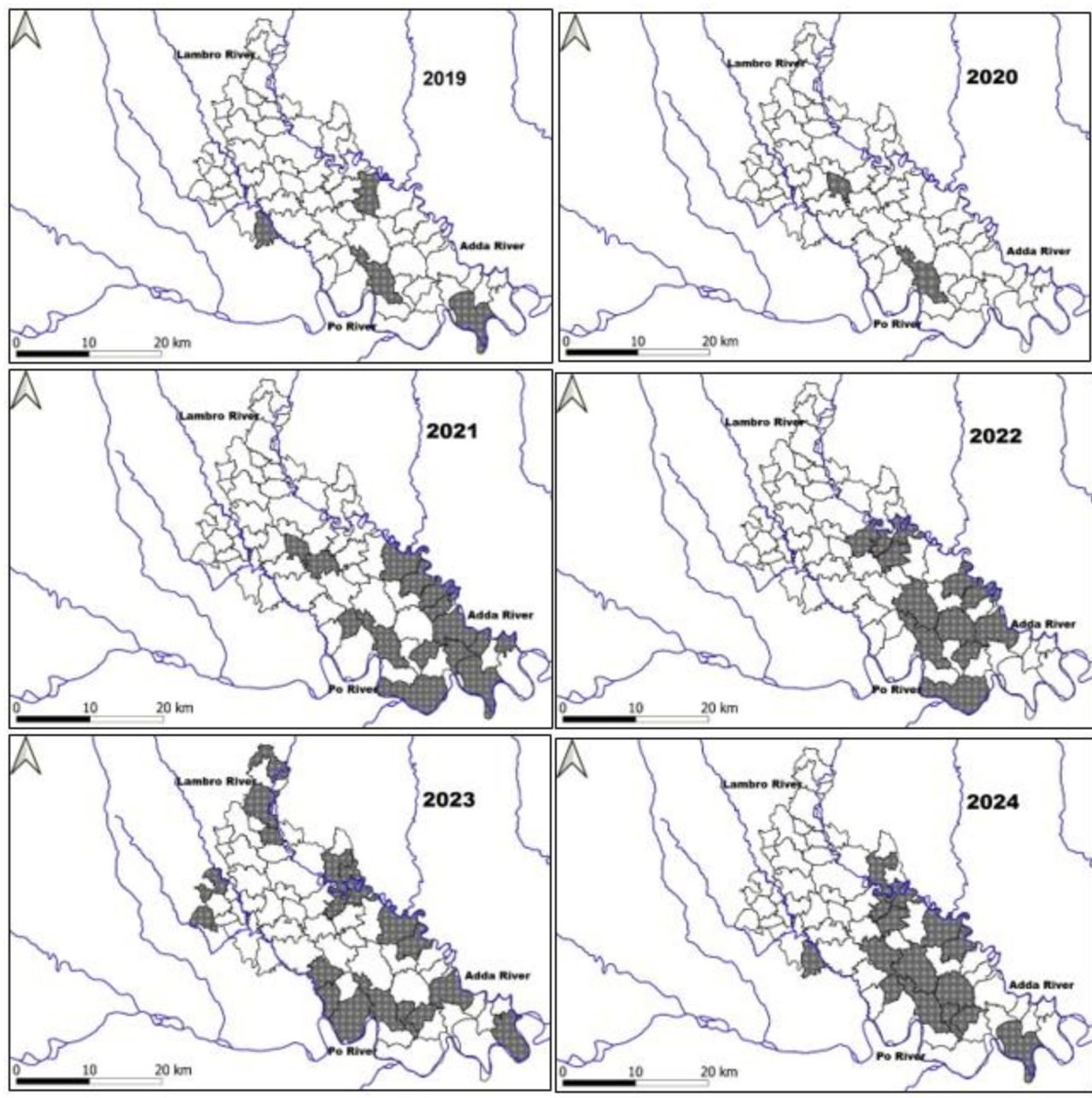


Figure 2. Time scan (2019-2024) of wolf colonization in the Lodi province (N-Italy, Lombardy)

Five environmental variables entered the model of wolf presence/absence of which four with significant effects ( $AICc = 64.63$ ;  $\Delta AICc = 23.93$ ); meadows, urban areas, and roads showed negative effects on the probability of wolf presence and urban green areas positive (Table III). Wetlands had also a positive but not significant effect. The explained deviance ( $D^2$ ) of the model was 0.39 and the ROC curve showed a good model performance ( $AUC = 0.89$ ; CL 95% 0.80-0.96; Figure 3). The model correctly classified 82.5% of the original cases (75.0% of the presence and 88.6% of the absence). No collinearity resulted among the selected variables.

Table III Results of the GLM on the presence (1) and absence (0) of the wolf in the municipalities of the Lodi province (LCL: Lower Confidence Limit 95%; UCL: Upper Confidence Limit 95%).

Variables	Coefficients	SE	LCL	UCL	Wald	P	Exp(b)	VIF
Meadows	-0.2	0.07	-0.4	-0.1	6.52	0.011	0.83	1.4
Urban areas	-0.5	0.18	-0.9	-0.2	7.98	0.005	0.61	2.0
Urban green areas	2.7	1.17	0.8	5.3	5.14	0.023	15.17	3.2
Roads	-1.1	0.43	-2.0	-0.3	6.29	0.012	0.34	2.0
Wetlands	1.4	1.09	-0.5	3.9	1.75	0.186	4.24	1.2
Intercept	3.4	1.11	1.5	5.9	9.09	0.003	29.01	

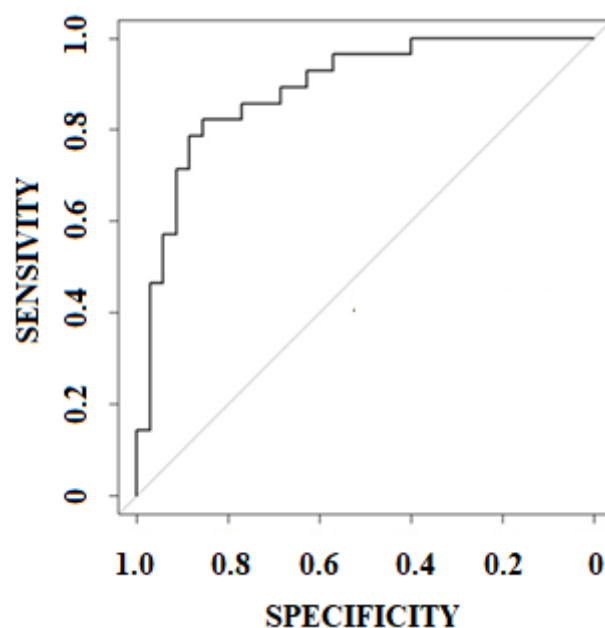


Figure 3. Roc curve of the GLM for wolf presence/absence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly)

Six environmental variables entered the model of wolf stable presence in the municipalities of Lodi province ( $AICc = 48.24$ ;  $\Delta AICc = 20.5$ ), of which five (Wetlands, Arable lands, Tree crops, Poplars, and Water basins) had positive and significant effects; Urban areas also had a positive but not significant effect (Table IV). The explained Deviance of the model was 0.949 and the ROC analysis showed an excellent discrimination ability of the model ( $AUC = 0.92$ ;  $CL95\% = 0.82-0.99$ ;  $P < 0.0001$ ) (Figure 4). The model correctly classified 92.1% of the total cases (98.0%



of sporadic presence or absence and 71.4% of regular presence). The variables that entered the model showed no collinearity.

Table IV. Results of the GLM on the stable presence (1) and sporadic presence (0) of the wolf in the municipalities of the Lodi province (LCL: Lower Confidence Limit 95%; UCL: Upper Confidence Limit 95%).

Variables	Coefficients	SE	LCL	UCL	Wald	P	Exp(b)	VIF
Wetlands	5.7	1.99	2.40	10.4	8.34	0.004	2.97	1.2
Urban areas	0.2	0.13	-0.01	0.5	2.91	0.088	1.25	2.0
Arable lands	0.3	0.12	0.10	0.6	7.63	0.006	1.41	3.2
Tree crops	2.7	1.00	1.00	5.4	7.36	0.007	1.54	2.0
Poplars	0.5	0.23	0.20	1.1	5.34	0.021	1.69	1.4
Water basins	1.5	0.65	0.20	2.9	4.90	0.027	4.34	1.4
Intercept	-30.5	10.84	-56.50	-13.1	7.87	0.005	<0.0001	

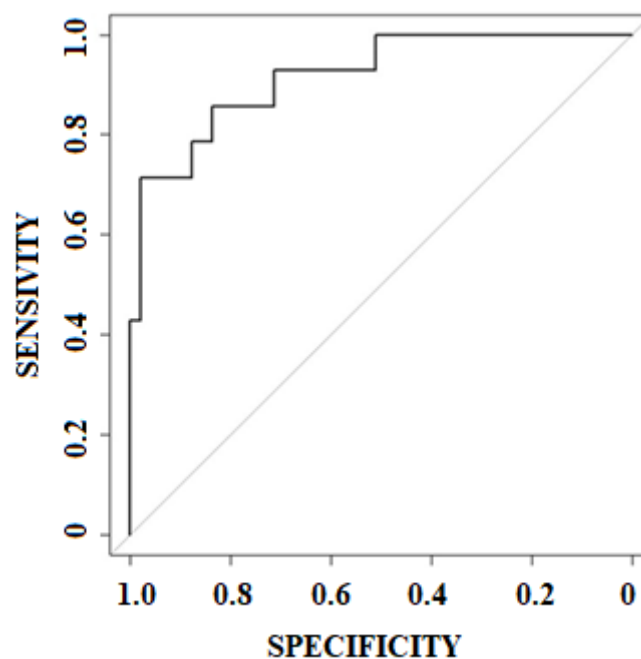


Figure 4. Roc curve of the GLM for wolf stable presence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly)

The model predicted a probability of stable presence of the specie  $> 0.5$  in 10 municipalities for a total of 160.22 km<sup>2</sup> and a probability  $> 0.7$  in 6 municipalities (94.5



km<sup>2</sup>). The municipalities with the highest probability of stable presence were located along the Po and Adda rivers and on the hills (Figure 5).

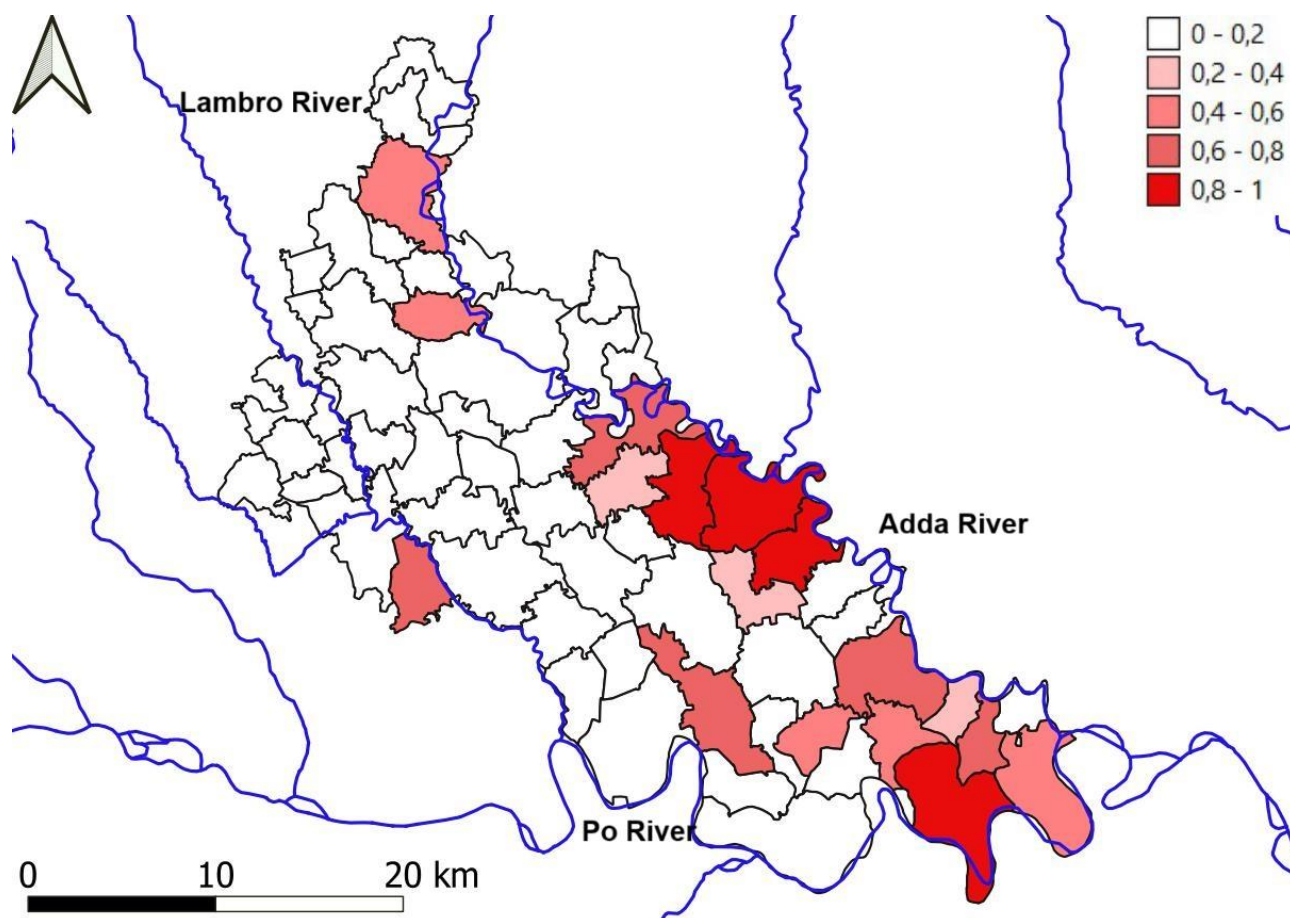


Figure 5.- Stable presence probability map for the wolf in the municipalities of the Lodi province (NW-Italy, Lombardy)

## Discussion

Wolf populations have been steadily and rapidly increasing over a large part of their distributional range for about 20 years (Mech 2017) and during this time they have recovered most of the areas lost between the 18th and 20th centuries mainly due to persecution and competition with humans (Chapron *et al.* 2014; Fardone *et al.* 2025). This first phase of the recolonisation process firstly concerned montane and peri-mountainous areas and then less elevated areas characterized by high wildness in northern Europe (i.e. Northern Poland; Jedrzejewski *et al.* 2004); in Italy this second phase of wolf population consolidation concerned the Ticino valley, one of the few

Italian rivers that provides an ecological corridor between the Alps and the Po Valley (Dondina *et al.* 2020; Fardone *et al.* 2025). The expansion of the species is still in rapid progress and the wolf is effectively colonizing the Po Valley, one of the most densely populated areas in Europe (Fardone *et al.* 2025).

This new phase of the wolf's expansion is quite different from previous ones, which had simple explanations linked to socio-cultural factors such as the positive effects of legal protection, the gradual abandonment of the Apennine mountains by man and the consequent increase in natural habitats and prey, and the constant reduction in the number of hunters and poachers in recent decades (Haller and Bender 2018). The recolonization of the Po Valley, an area where the species became extinct at the end of the 18th century, but from which it had almost disappeared two centuries earlier, presents completely new characteristics, since it is the most densely populated area in Italy and one of the most densely populated in Europe (Livani *et al.* 2023). The Po Plain is a highly urbanised and infrastructurally developed area, which, at least at first sight, lacks the environmental characteristics suitable for this predator outside of parks and nature reserves. (Zimmermann *et al.* 2014, Bassi *et al.* 2015, Zanni *et al.* 2023, Fardone *et al.* 2025) Although the recolonisation of the entire European range of the wolf is still in progress, and although some parts of the historical range can only be recovered by reintroduction (e.g. Great Britain) it is clear that if the species were to colonize the Italian Po Valley, it would be able to reclaim the whole of Europe, with the exception of the more densely urban areas.

North of the Po river, the Province of Lodi was one of the first areas where the wolf was recorded, while in the plains of the neighbouring Emilia-Romagna region (province of Piacenza), the presence of wolves had already been reported since 2012 (AA VV 2018). The diffusion of wolves in our study area do not seems a continuous and progressive phenomenon, but rather a sudden and relatively widespread one. All sighting in 2019 occurred in autumn, all including young individuals in the dispersal phase appearing in relatively distant localities. In the following year a decrease in reports and colonized territories was observed, despite the replication of reproduction

in one of the first colonised municipality. Then, between 2021 and 2023, the species spread to all the municipality bordering the Po river to the south, Adda river to the east and hilly areas and the Lambro river along the western boundary of the province. This expansion, during which we recorded at least 4 new reproductions and recurring reproductions are confirmed in first-settlement areas, is followed by a new phase of slight contraction in 2024. The pattern here described seems to reflect a progressive "pulse" process of recolonisation, in which several young individuals settle, albeit for a limited period, in new municipalities, while adult reproducing pairs establish themselves in municipalities that, having been acquired in previous years, have proved more suitable to host adult pairs on a stable basis.

### *Population metrics*

Although the results of our study are also based on opportunistic data collection, they seem to confirm what is known in the literature about wolf populations in Europe. It is therefore likely that some of the following generalizations are largely reliable and useful for understanding wolf population dynamics in densely populated areas. From 2021 to 2024, the average wolf density in the study area was 0.89 ind./km<sup>2</sup> (range = 0.73-1.09 ind./km<sup>2</sup>), a lower value than that found in protected areas in Spain (1.7 ind./km<sup>2</sup>; Nakamura *et al.* 2021, 2.9 ind./km<sup>2</sup>; Blanco and Cortes 2007), Poland (2.0-2.6 ind./km<sup>2</sup>) and Italy (4.7 ind./km<sup>2</sup>; Apollonio *et al.* 2004) and more like to densities found where the species is culled, such as in Belarus (0.9-1.5 ind./km<sup>2</sup>; Okarma 1998), Sweden (0.15 ind./km<sup>2</sup>; Dalerum *et al.* 2020) and Finland (0.30-0.35 ind./km<sup>2</sup>; Kojola *et al.* 2006). The litter and pack data also show some similarities with those collected in Europe. Our estimate of an average litter size of 4.8 cubs is consistent with data from Sidorovich *et al.* (2007), who reported average litter sizes of 4.8-7.7 in Belarus. The estimated size of our packs (8-9 individuals) is also compatible with data from Spain (6.2; Nakamura *et al.* 2021, 6.5; Barrientos 2000; 9.3 Fernandez-Gil 2013), Poland (4-5; Okarma 1998), France (average 3.8 min=2 max=12; Duchamp *et al.* 2012), Italy (average 4.2, max=7; Apollonio *et al.* 2004).

The general comparison between our population metrics and those available on European populations seems to suggest that some post-reproductive parameters are rather similar, while population density data are close to those recorded for northern population where regular culling and the trophic constraints of high latitude habitats can negatively affect the distribution and abundance of the wolf. These data suggest that our population could be in full demographic expansion, and that it may increase in the coming years.

### *Resident vs. dispersing wolves: differences in habitat features*

The presence of the wolf is associated with a triad of variables (extent of poplar groves, water basins and scrubland) that define the riparian and floodplain environments in which the species can find shelters, while it is negatively affected by the area of meadows. As this variable is directly correlated with the area of wooded environments, water basins and protected areas, we believe that the figure reflects a wolf choice for natural areas not fragmented by crops such as meadows. Overall, the GLM model confirms the univariate comparison and describes an easily interpretable environmental context, where roads and urban areas, together with meadows, are unfavourable predictors for the wolf, while urban green areas contribute positively and significantly to the model. In the Lodi province, many towns and villages are crossed by rivers and canals which, close to settlements, often preserve green areas and forests that far from towns have been removed. We consider it likely that this variable, which is indeed positively correlated with urban areas ( $r=0.43$ ,  $n=63$ ,  $p<0.0001$ ), makes a positive contribution to the model by describing areas of limited anthropic disturbance in contexts of high population density.

The environmental characteristics that influence the stable vs. irregular presence of wolves in municipalities are slightly different. The tree cover in wetlands, guaranteed by natural forests, but also by poplar groves and reforestation, is higher where the wolf has a regular and stable presence; however, the stability of wolf presence also seems

to be positively influenced by extensive cropland. In our study area, the alternation between small protected areas and large areas of arable land is a dichotomous phenomenon ( $r = 0.46$ ,  $n = 63$ ,  $p < 0.0001$ ): at the border of the first category, the second suddenly begins without transitional areas with gradually decreasing wildness. The wolf is likely to settle permanently in the small protected areas, even in the proximity of urban areas, where large open areas allow effective control of sources of danger or disturbance. The GLM model largely confirms what was found in the univariate comparison, attributing a positive influence to wetlands and water basins with high tree cover and extensive surrounding crops. Even urban areas, whose effect is not significant, seem to have a positive effect on the stable presence of the species, confirming what was discussed above. The contribution of wetlands and water basins to the model is important because the dynamics of wolf distribution in the study area is also influenced by the availability of food resources.

In Europe, wolf presence and abundance are correlated with the availability of wild ungulates, a trophic resource that is scarce in the study area. Where wild ungulates are scarce, livestock can become a trophic resource of considerable importance for the wolf (Meriggi and Lovari 1996, Meriggi *et al* 2011, Zlatanova *et al.* 2014). However, in the province of Lodi, as in the whole of the Po Valley, livestock is not left to graze in the open, but is bred and kept in stables, and is therefore not available to wolves. Based on preliminary scat analyses, the main food resource of the wolf in our area is the coypu *Myocastor coypu* and, to a much lesser extent, the cottontail *Sylvilagus floridanus* (Torretta *com pers*; *M. coypus* = 98% *S. floridanus* = 2.0%  $n = 28$ ). Coypus are common in the province of Lodi because of the dense water network and are widespread in wetlands and water basins; the contribution of these variables to the model may also indicates the presence of food resources, which are fundamental for the survival of the species. The hypothesis that the coypu is a key element in the successful expansion of the wolf in the southern provinces of the Lombardy Region is supported by its density in our study area, which is by far the highest in the region (about 131.9 ind./km<sup>2</sup>; Balestrieri *et al* 2015, recalculated).



We observed similarities and differences with literature data and recent analyses of the environmental suitability of the entire Po Valley (Dondina *et al* 2020, De Feudis *et al* 2025; Fardone *et al* 2025). Our study confirms the importance of forest cover, even of small sizes, in providing the presence and stability of wolf packs, but contrary to what has been observed by other authors, in our case a stable presence of the wolf does not seem to be negatively conditioned by anthropogenic elements such as roads, motorways and railways. Good tolerance to human settlements has also been found in Tuscany, particularly in the areas recently colonized by wolves; this can be explained by the increase in the wolf population and the reduction of more natural areas not yet occupied where dispersing wolves can settle (Zanni *et al.* 2023). The environmental choices of local wolf populations, also due to the ecological plasticity of the species are highly variable, but in most published studies roads, urban areas and crops reduce the connectivity of populations by acting as important barriers to wolf dispersal (Jedrzejewski *et al.*, 2004; Rodríguez-Freire and Crecente-Maseda, 2008; Dondina *et al.*, 2020; De Feudis *et al.* 2025). In our case, despite the high incidence of mortality due to vehicle collisions, the expansion of the road network does not seem to affect the habitat choices when wolves stabilize their presence. If other environmental conditions are met, the wolf still settles near road networks, despite their negative influence on reproduction that curbs its spreading.

## Conclusions

The colonisation of urbanised lowland areas is a case study for the wolf, which is once again threatened in Europe by the downgrading of its conservation status. This reconquest could be the final stage in the recolonization of the historic European range, and the beginning of a phase of coexistence between humans and a large carnivore. The low densities observed in our study area are lower than those recorded in protected areas and similar to those of the northern population; the low density of the latter reflects culling effects and the trophic constraints of high latitude habitats, suggesting a further potential for expansion of the species in the Po Valley. The presence of wolves



is mainly influenced by natural or artificial forest formations, while the stability of a population is also favoured by wetlands, abandoned reservoirs and the presence of green areas close to inhabited areas; residual protected forests and wetlands are a refuge for wolves and favour their settlement even close to human settlements. In addition, wetlands and reservoirs support abundant populations of coypu, a prey species that, according to preliminary analyses, constitutes almost the entire diet of the wolf in our study area. Contrary to other reports, the wolf does not avoid the network of motorways, roads and railways, even though mortality of young wolves can reach up to 75% of annual productivity. Road killing is increasing and may be linked to the use of rodenticides in agriculture: indeed, recent research shows that almost all wolves hit by vehicles tested positive for warfarin and other anticoagulants (Musto *et al.* 2024).

On the basis of these data, we believe that the wolf will expand in the province of Lodi as far as the Milan area, where the motorway network may act as a dispersal sink, preventing the species from reaching the Alps and existing mountain populations.

The local population we studied is not currently threatened, and the recovery of the Lodi plain depends mainly on roadkill; since roadkill of young wolves is high in areas with a stable wolf presence, mitigating this impact by creating culverts and protected passages could represent a limited and economically sustainable approach that would guarantee population productivity, promote juvenile dispersal and ultimately the conservation of new wolf populations in the lowlands of Europe.

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**APPENDIX A.** Habitat characteristics of the study area. Data are the total surface for the municipalities of the Province of Lodi.

Variable	total area (ha)	%	min	max
Cultivated land	61166.5	74.3	170.2	2567.4
Urban areas	5119.1	6.2	6.1	590.1
Woodland	3121.7	3.8	1.9	206.7
Reforestation, poplar groves	2939.0	3.6	0	437.8
Factories	2509.4	3.0	0.8	207.8
Farmhouse	1925.4	2.3	4.7	92.8
River and riparial habitat	1870.9	2.3	0	242.4
Shrubland	1642.4	2.0	1.2	136.5
Roads and highways	1268.3	1.5	0	156.0
Urban parks	338.3	0.4	0	63.2
Water basin	252.3	0.3	0	48.1
Natural habitat	133.3	0.2	0	25.4
Landfills and degraded areas	66.7	0.1	0	11.7

661Table 1. Habitat variables for 63 municipalities in the province of Lodi.

Municipality	Area (ha)	Urbanized areas	Hamlets	Farmhouse	Factories	Motorway and roads	Railways	Gravel pits	Urban green areas	Horticulture	Untilled land	Crops	Orchards	Ricefields	Poplar groves	Meadows	Woodlands	Riparial woodlands	Shrublands	Rivershed bushes	Riverbanks bushes	Riverbeds	Wetland vegetation	River area	Water basins	River lenght (m)	Protected areas	
Abbadia Cerreto	620.3	10.1	0.6	4.8	18.0		0.0	0.0	0.3	0.0	0.0	309.3	0.0	0.0	13.8	227.8	1.9	16.6	4.0	1.0	0.0	0.0	5.9	5.6	0.7	1631.8	7.8	
Bertonico	2084.7	31.5	9.5	5.0	137.1		13.4	0.0	0.0	0.0	0.0	1267.8	0.0	0.0	156.5	242.3	8.6	115.2	11.5	8.1	0.0	9.4	23.2	43.6	0.0	5834.4	0.0	
Boffalora d'Adda	81.3	25.0	6.8	7.4	26.6		0.0	0.0	2.0	0.0	0.0	1.2	473.7	0.0	0.0	7.6	137.1	12.4	45.1	11.1	13.3	0.0	17.7	1.0	20.7	0.0	3287.1	0.0
Borghetto Lodigiano	2365.9	95.8	16.0	20.7	73.7		37.9	13.9	0.9	0.0	0.0	3.1	1452.6	0.8	107.8	38.8	436.8	5.3	38.3	3.8	0.0	0.0	0.7	6.3	0.0	248.1	25.3	
Borgo San Giovanni	751.0	44.1	4.8	3.9	87.8		5.3	0.4	12.4	1.1	0.0	10.1	473.2	0.0	0.0	16.0	45.6	2.9	17.9	11.4	1.9	0.2	0.0	0.8	11.2	0.0	1315.4	33.8
Brembio	1709.7	59.1	4.6	16.3	71.2		1.7	2.2	0.0	2.1	4.6	6.2	1235.1	0.0	0.0	0.8	270.9	0.9	26.5	3.2	0.0	0.0	0.0	4.4	0.0	0	6.2	
Camairago	1278.2	15.6	3.3	10.2	31.5		1.0	0.0	26.6	0.9	10.6	3.8	803.3	0.2	0.0	59.7	146.6	34.0	78.0	6.8	0.0	2.3	4.5	0.1	38.6	0.4	7738.5	0.0
Casaletto Lodigiano	975.9	54.4	1.7	2.4	38.2		11.9	0.0	0.0	1.4	0.0	0.4	667.7	0.0	83.0	0.3	82.3	1.3	13.5	2.7	0.9	0.0	0.4	0.0	13.4	0.0	2959.3	0.0
Casalmaiocco	471.8	52.0	1.9	1.5	39.5		20.5	0.0	0.0	7.4	18.8	4.5	294.1	0.0	0.0	0.0	25.1	0.7	5.6	0.0	0.0	0.0	0.0	0.1	0.0	0	22.7	
Casalpusterleno	2563.2	236.6	9.1	21.3	197.6		20.7	21.3	1.6	22.9	0.8	21.9	1741.8	0.4	0.0	18.1	170.3	3.1	18.7	34.9	0.0	2.3	0.0	1.1	15.6	0.0	0	0.0
Caselle Landi	2602.3	44.9	42.6	17.6	36.9		0.2	0.0	9.1	7.1	37.6	0.8	1660.7	0.9	0.0	436.0	14.5	3.3	35.4	12.3	2.9	43.1	0.0	0.8	195.3	0.3	9091.8	21.0
Caselle Lurani	768.4	59.3	4.5	2.1	23.7		1.4	0.0	0.0	4.3	0.0	2.9	334.4	0.0	237.4	3.0	65.4	0.0	16.2	2.2	0.0	4.2	0.2	0.0	7.1	0.0	0	0.3
Castelnuevo B. Adda	2033.7	66.5	8.3	8.9	34.1		1.6	0.0	3.9	4.1	23.0	0.1	1312.7	0.6	0.0	215.0	13.8	0.0	37.6	16.9	16.5	42.8	29.9	1.3	195.2	0.9	6303.2	23.6
Castiglione d'Adda	1298.8	98.1	9.3	8.3	35.6		0.9	0.0	2.2	5.1	0.0	3.9	889.3	0.0	0.0	17.8	104.6	0.8	89.5	7.8	1.1	6.1	0.4	5.3	9.6	3.0	2329	9.8
Castiraga Vidardo	504.2	50.5	17.2	2.6	36.5		1.5	0.0	0.0	4.9	0.0	7.2	314.3	0.0	9.7	4.6	13.5	0.0	30.8	1.9	0.8	0.3	0.0	0.9	7.1	0.0	4789.1	0.0
Cavacurta	710.2	22.1	7.5	10.1	13.2		2.4	0.0	0.6	1.5	1.7	0.2	518.6	0.0	0.0	3.8	107.6	1.0	13.0	2.7	0.0	3.7	0.0	0.5	0.0	0.0	0	6.6
Cavenago d'Adda	1611.0	57.2	7.8	8.6	66.6		13.5	0.0	0.1	3.7	0.0	3.3	892.7	0.0	105.2	34.2	186.5	22.0	117.6	9.8	10.1	0.0	2.7	25.4	44.3	0.0	8370.7	1.9
Cervignano d'Adda	407.2	35.3	5.8	1.2	22.9		2.7	0.0	0.0	0.0	0.0	0.8	211.0	1.3	0.0	0.3	105.0	0.0	13.9	0.4	0.0	0.0	0.0	0.0	6.6	0.0	0	0.0
Chignolo Po	2340.7	90.4	83.9	11.4	92.1		5.0	13.7	3.7	11.8	5.2	12.6	1221.9	4.6	309.3	228.7	77.7	54.7	23.9	26.2	0.8	32.7	1.1	0.3	28.8	0.2	3976.4	0.0
Codogno	2088.5	246.7	22.0	29.1	221.1		45.7	24.5	4.1	24.3	3.3	16.2	1302.4	1.2	0.0	0.0	103.3	10.9	11.3	14.8	0.0	7.4	0.0	0.4	0.0	0.0	0	0.0
Comazzo	1281.2	38.7	9.6	5.3	24.3		27.4	0.0	0.2	3.7	2.4	4.6	666.9	0.0	73.4	48.8	141.0	81.9	68.4	14.5	4.0	2.9	4.8	3.0	54.2	0.0	4464.2	0.0
Corneigliano Launese	570.4	61.7	4.7	10.8	58.8		13.6	0.0	0.0	3.5	0.2	4.9	257.3	0.0	34.2	18.6	72.8	0.0	13.6	3.5	0.0	2.4	0.0	0.0	9.7	0.0	0	0.0
Corno Giovine	994.3	31.8	8.8	9.0	22.6		1.8	0.0	2.6	1.2	6.3	3.1	797.6	2.3	0.0	4.3	52.7	6.0	13.5	0.5	1.0	6.8	0.2	0.0	22.1	0.0	0	0.0
Cornovecchio	653.6	6.8	0.3	9.4	7.7		0.7	0.0	0.4	2.1	14.7	1.1	517.2	0.0	0.0	3.9	6.0	9.7	37.2	0.0	5.1	5.7	2.9	0.0	22.8	0.0	1741.7	58.8
Corte Palasio	1569.0	35.4	4.3	10.5	50.5		2.2	0.0	0.6	0.0	0.0	1.0	883.1	0.0	0.0	51.6	369.6	4.1	54.5	9.5	15.6	0.0	3.5	17.5	54.8	0.8	5956.3	17.5
Crespianica	703.7	42.1	2.4	4.7	46.7		0.6	0.0	0.0	0.7	0.0	0.9	390.3	0.0	11.3	17.1	180.9	0.0	1.9	4.1	0.0	0.0	0.0	0.0	0.0	0.0	0	5.5
Fombio	740.2	48.0	4.8	3.3	93.1		14.9	12.5	1.0	8.1	0.6	13.7	484.8	0.0	0.0	0.0	12.1	8.7	15.9	6.0	0.0	8.4	0.0	0.0	4.4	0.0	0	0.0
Galgagnano	601.6	19.5	3.5	3.6	24.2		1.3	0.0	1.7	1.6	0.0	1.9	392.7	0.0	0.0	5.5	80.7	19.2	30.3	5.8	4.0	0.0	1.8	0.0	4.3	0.0	397.9	0.0
Graffignano	1093.0	62.3	18.3	7.0	35.4		1.2	0.0	0.3	5.7	0.0	1.7	602.2	38.4	52.3	14.1	118.2	97.1	18.3	2.1	0.0	0.0	0.0	0.0	18.6	0.0	4059.9	0.3
Guardamiglio	1044.5	52.0	22.2	2.2	104.7		24.3	0.0	0.8	2.5	16.1	5.2	640.3	0.0	0.0	7.4	12.2	5.2	18.6	6.6	2.1	34.2	19.2	0.0	68.7	0.0	0	2.9
2vraga	1238.1	69.9	0.2	9.7	57.6		16.6	15.9	2.0	4.2	0.0	18.9	753.2	0.0	17.2	10.7	225.9	0.9	15.0	5.0	0.1	0.5	0.0	0.0	14.6	0.0	1218.2	0.2
Lodi	4141.0	495.9	34.1	43.8	321.8		135.2	20.8	18.1	73.9	15.3	22.3	2099.9	8.2	25.9	108.7	418.3	76.2	108.5	44.2	6.8	2.4	2.5	0.9	57.1	0.2	8868.9	1.0
Lodi Vecchio	1646.4	98.3	4.3	15.6	94.8		36.0	23.0	0.5	7.6	2.9	31.0	1088.0	1.9	91.1	10.7	86.6	4.9	27.5	13.3	0.0	0.0	0.0	0.0	8.5	0.0	343.7	10.1
Maccastorna	575.0	3.7	2.4	2.9	40.4		0.0	0.0	8.3	0.0	62.7	0.7	321.8	0.0	0.0	21.9	10.2	1.1	31.9	11.0	0.7	13.2	3.4	0.0	38.8	0.0	2967.6	0.0
Mairago	1125.6	38.1	2.8	7.9	34.2		6.1	0.0	23.1	1.4	0.0	2.0	801.5	0.0	40.5	18.0	77.4	8.4	49.2	7.0	0.0	0.0	0.0	0.0	8.0	0.0	0	53.7
Maleo	1984.8	68.2	8.9	24.8	86.5		20.1	12.2	22.1	5.4	1.1	7.3	1577.1	0.0	0.0	10.6	72.3	16.5	25.0	7.0	0.4	6.5	0.0	0.0	12.9	0.0	2286.5	18.9
Marudo	420.6	38.1	1.2	3.0	20.3		0.0	0.0	0.0	0.0	0.0	1.0	241.8	0.0	63.9	18.4	21.8	0.0	7.7	0.0	0.0	1.6	0.0	0.0	1.7	0.0	0	0.0
Massalengo	848.3	78.6	1.2	8.0	73.5		8.5	2.1	0.5	1.6	0.0	3.8	572.7	0.0	8.0	1.5	71.7	1.0	12.9	1.5	0.0	0.0	0.0	0.0	0.0	0	24.2	
Meleti	739.1	13.8	4.7	11.6	16.4		0.5	0.0	0.0	2.9	14.3	2.4	589.2	0.0	0.0	28.2	8.0	1.6	20.9	4.6	0.0	7.9	0.1	0.0	12.2	0.0	474.1	0.2
Merlino	1073.9	29.1	6.9	5.1	49.2		27.5	0.0	0.0	9.5	0.0	3.3	647.3	0.0	24.9	37.4	135.9	15.7	41.4	5.3	1.5	1.1	3.0	1.2	28.7	0.0	1452.2	0.0
Montanaso Lombardo	952.9	54.8	5.2	11.7	89.9		18.9	0.0	48.1	5.6	10.5	4.9	425.7	10.3	0.0	6.5	93.8	69.1	24.9	8.5	10.6	1.9	6.7	0.0	33.9	2.1	2530.8	3.3
Mulazzano	1559.1	88.1	7.4	12.0	49.3		20.6	0.0	1.2	7.2	1.5	1.7	1098.2	0.9	0.0	27.8	178.5	5.2	27.5	10.0	0.0	0.6	0.0	0.0	21.4	0.0	0	18.6
Orio Litta	979.1	54.6	3.3	5.6	34.6		2.1	0.0	21.0	4.8	0.0	1.5	580.0	0.3	90.2	29.6	61.1	12.0	18.7	8.8	1.5	19.6	2.6	0.0	27.0	0.0	73.6	48.8
Ospedaletto Lodigiano	850.3	35.4	12.3	11.6	64.2		39.3	14.7	0.5	15.4	0.0	11.8	501.9	0.0	52.3	27.5	35.8	0.6	7.6	19.3	0.0	0.0	0.0	0.0	0.0	0.0	0	0.0
Ossago Lodigiano	1153.4	28.8	2.0	11.0	43.3		0.0	0.0	0.0	1.8	0.6	1.9	822.0	0.0	96.6	11.6	118.0	0.0	14.9	0.0	0.0	0.0	0.0	0.0	0.8	0.0	0	14.4
Pieve Fissiraga	1227.5	30.4	14.6	16.4	106.1		45.3	11.1	0.0	2.4	0.0	6.1	809.9	0.0	9.6	2.7	141.5	1.6	27.4	1.6	0.0	0.0	0.0	0.0	0.9	0.0	0	3.1
Salerano sul Lambro	437.8	42.3	2.1	5.0	29.0		8.1	0.0	0.0	2.8	0.0	2.1	254.5	5.5	0.7	3.5	49.2	0.0	22.8	0.5	1.2	0.0	0.0	0.0	8.5	0.0	2839.4	48.4
S. Colombano Lambro	1656.3	135.1	72.3	6.7	87.7		4.7	0.0	0.2	0.0	0.3	0.3	584.9	281.6	0.0	49.3	134.8	170.9	9.2	42.3	0.6	0.0	0.0	0.0	23.2	0.0	6634.4	0.2
San Fiorano	897.2	54.2	6.5	11.0	35.2		0.6	4.0	0.0	47.3	23.2																	

Cod	Data	Year	Month	Location	Coordinates	Source	N
1	01/09/2019	2019	9	Graffignana	45°12'25.0" 9°27'03.8"	sighting	1
2	16/11/2019	2019	11	Caselle Landi-Corno	45°06'56.9" 9°46'06.3"	sighting	1
3	16/11/2019	2019	11	Caselle Landi	45°06'03.2" 9°47'31.7"	sighting	1
4	13/12/2019	2019	12	Turano Lodigiano	45°13'42" 9°38'07"	sighting	6
5	05/02/2020	2020	2	S martino Strada	45°15'55.6" 9°31'52.2"	sighting	1
6	12/07/2020	2020	7	Massalengo	45°15'49.0" 9°29'11.3"	sighting	2
7	09/09/2020	2020	9	Somaglia	45°08'36.82" 9°39'39.17"	sighting	1
8	18/01/2021	2021	1	Somaglia	45°08'34.88" 9°39'21.36"	sighting	1
9	03/02/2021	2021	2	Lambrinia	45°09'53.9" 9°31'42.9"	sighting	1
10	15/03/2021	2021	3	Caselle Landi	45°06'03.3" 9°47'31.8"	predation	1
11	19/03/2021	2021	3	Maleo	45°09'02.17" 9°46'48.36"	roadkill	1
12	22/03/2021	2021	3	Ospedaletto Lodigiano	45°10'22.76" 9°34'57.57"	sighting	1
13	26/03/2021	2021	3	San Rocco al Porto	45°04'44.1" 9°43'54.7"	sighting	2
14	26/03/2021	2021	3	San Rocco al Porto	45°04'42.7" 9°41'45.4"	sighting	1
15	02/04/2021	2021	4	Somaglia	45°08'43.8" 9°39'11.5"	scats	1
16	08/04/2021	2021	4	Castiglione	45°13'42.0" 9°42'19.1"	sighting	2
17	12/04/2021	2021	4	Maccastorna	45°08'43.32" 9°50'37.02"	sighting	1
18	16/04/2021	2021	4	Bertonico	45°15'10.25" 9°40'55.05"	predation	1
19	25/04/2021	2021	4	S.Stefano L-C Giovine	45°07'45.80" 9°44'48.20"	predation	1
20	29/04/2021	2021	4	S.Stefano L-C Giovine	45°07'32.5" 9°45'02.9"	sighting	1
21	29/04/2021	2021	4	Caselle Landi	45°06'05.4" 9°47'03.9"	sighting	1
22	13/05/2021	2021	5	Somaglia	45°08'40.7" 9°39'13.5"	scats	1
23	15/05/2021	2021	5	Somaglia	45°08'51.7" 9°39'15.3"	sighting	3
24	18/05/2021	2021	5	Somaglia-Casale	45°09'23.90" 9°38'44.91"	sighting	2
25	22/05/2021	2021	5	Somaglia	45°08'44.3" 9°39'11.3"	sighting	1
26	24/05/2021	2021	5	Somaglia	45°08'48.0" 9°39'09.0"	sighting	1
27	01/06/2021	2021	6	Castelgerundo	45°12'24.09" 9°45'38.08"	scats	1
28	13/06/2021	2021	6	Ossago Lodigiano	45°14'30.8" 9°31'55.6"	sighting	2
29	16/06/2021	2021	6	Bertonico	45°15'10.25" 9°40'55.05"	sighting	2
30	17/06/2021	2021	6	Somaglia	45°08'39.16" 9°39'51.55"	predation	1
31	23/06/2021	2021	6	Pizzighettone	45°10'07.4" 9°47'42.9"	sighting	2
32	06/07/2021	2021	7	Pizzighettone	45°10'31.0" 9°46'19.0"	sighting	2
33	30/08/2021	2021	8	S Fiorano	45°07'22.1" 9°42'54.6"	sighting	1
34	20/09/2021	2021	9	Massalengo	45°16'07.3" 9°30'41.1"	sighting	4
35	27/10/2021	2021	10	Caselle Landi	45°05'23.0" 9°47'01.8"	predation	2
36	11/11/2021	2021	11	Cavacurta	45°11'06.9" 9°44'28.2"	sighting	2
37	15/11/2021	2021	11	Somaglia	45°08'53.6" 9°39'15.8"	sighting	1
38	22/11/2021	2021	11	Formigara	45°13'16.37" 9°46'51.34"	predation	1
39	25/11/2021	2021	11	Formigara	45°13'16.37" 9°46'51.34"	predation	1
40	27/11/2021	2021	11	Montodine	No data	roadkill	1
41	29/11/2021	2021	11	Pizzighettone	45°13'11.30" 9°47'18.13"	sighting	1
42	01/12/2021	2021	12	Pizzighettone-Maleo	45°10'28.9" 9°46'26.0"	sighting	1
43	02/12/2021	2021	12	Cornovecchio	45°08'16.3" 9°48'35.3"	sighting	2
44	12/12/2021	2021	12	S Fiorano	45°08'13.2" 9°42'43.7"	sighting	2
45	15/12/2021	2021	12	S. Colombano Lambro	45°10'31.6" 9°28'04.8"	sighting	4
46	05/01/2022	2022	1	Maleo	45°08'28.4" 9°47'09.7"	sighting	2
47	22/02/2022	2022	2	Somaglia	45°08'39.7" 9°39'08.3"	sighting	1
48	18/04/2022	2022	4	Codogno	45°10'12.0" 9°43'28.2"	sighting	1

713	49	13/03/2022	Manuscript body			Borghetto Lodigiano	45°12'24.1" 9°29'59.6"	sighting	1
714	50	22/06/2022	Download DOCX (637.54 kB)			Casalpusterlengo	45°10'14.8" 9°39'20.4"	predation	1
715	51	23/06/2022	2022	6		Cavenago	45°17'01.4" 9°34'10.8"	sighting	1
716	52	28/06/2022	2022	6		Mairago	45°15'53.3" 9°35'01.7"	sighting	1
717	53	30/07/2022	2022	7		Bertonico	45°14'00.07" 9°38'58.76"	sighting	2
718	54	01/11/2022	2022	11		Camairago	45°12'14.8" 9°43'19.8"	sighting	1
719	55	02/11/2022	2022	11		San Fiorano	45°08'09.5" 9°42'51.0"	sighting	1
720	56	03/11/2022	2022	11		Maleo	45°10'36.5" 9°46'36.4"	roadkill	1
721	57	30/11/2022	2022	11		San Rocco al Porto	45°05'51.7" 9°43'37.1"	sighting	3
722	58	02/12/2022	2022	12		San Martino in Strada	45°16'50.3" 9°32'02.0"	sighting	3
723	59	01/01/2023	2023	1		Fombio	45°07'35.2" 9°41'14.5"	roadkill	1
724	60	02/01/2023	2023	1		Galgagnano	45°21'22.8" 9°27'40.6"	sighting	9
725	61	02/01/2023	2023	1		S. Colombano Lambro	45°10'48.7" 9°28'08.0"	predation	1
726	62	29/01/2023	2023	1		San Fiorano	45°08'22.2" 9°42'21.9"	uccisione	1
727	63	06/02/2023	2023	2		San Fiorano	45°08'22.2" 9°42'21.9"	predation	1
728	64	April 2023	2023	4		San Fiorano	45°08'38.2" 9°42'28.3"	predation	1
729	65	23/02/2023	2023	2		Maleo	45°09'34.21" 9°46'46.82"	sighting	4
730	66	30/04/2023	2023	4		San Fiorano	45°07'47.0" 9°42'53.3"	sighting	1
731	67	25/05/2023	2023	5		Valera Fratta	45°15'21.5" 9°19'29.4"	sighting	1
732	68	27/06/2023	2023	6		S. Colombano Lambro	45°11'04.2" 9°27'53.0"	sighting	2
733	69	28/06/2023	2023	6		Castelnuovo B. Adda	45°06'41.3" 9°51'10.8"	sighting	1
734	70	27/07/2023	2023	7		Casaletto lodigiano	45°17'45.7" 9°22'04.9"	sighting	1
735	71	27/07/2023	2023	7		Orio Litta	45°09'25.3" 9°33'13.6"	sighting	2
736	72	27/07/2023	2023	7		Castiglione d'Adda	45°13'46.2" 9°41'27.0"	sighting	3
737	73	01/08/2023	2023	8		Castiglione d'Adda	45°14'10.96" 9°42'22.34"	sighting	4
738	74	03/08/2023	2023	8		Castiglione d'Adda	45°13'37.7" 9°41'32.3"	sighting	1
739	75	16/08/2023	2023	8		Maleo	45°09'13.71" 9°48'54.88"	sighting	1
740	76	27/09/2023	2023	9		Cavenago d'Adda	45°17'32.4" 9°36'45.9"	sighting	3
741	77	27/09/2023	2023	9		Cavenago d'Adda	45°17'25.8" 9°37'01.0"	sighting	2
742	78	27/09/2023	2023	9		Cavenago d'Adda	45°17'25.8" 9°37'01.0"	sighting	2
743	79	21/10/2023	2023	10		Fombio	45°08'26.1" 9°40'34.1"	roadkill	1
744	80	24/10/2023	2023	10		S. Colombano Lambro	45°10'12.9" 9°28'43.6"	sighting	3
745	81	16/11/2023	2023	11		Senna Lodigiana	45°08'07.47" 9°34'20.28"	sighting	1
746	82	02/12/2023	2023	12		San Fiorano	45°08'22.2" 9°42'21.9"	sighting	3
747	83	No data	2023			Zelo Buon Persico	45°22'41.3" 9°26'54.6"	sighting	1
748	84	11/12/2023	2023	12		San Fiorano	45°08'22.2" 9°42'21.9"	sighting	3
749	85	No data	2023			Corte Palasio	45°18'07.2" 9°34'08.6"	sighting	1
750	86	No data	2023			Abbadia Cerreto	45°18'31.6" 9°36'01.7"	sighting	1
751	87	No data	2023			Turano Lodigiano	45°16'15.1" 9°38'49.3"	sighting	1
752	88	No data	2023			Bertonico	45°15'28.3" 9°40'01.8"	sighting	1
753	89	No data	2023			Bertonico	45°15'17.1" 9°40'28.3"	sighting	1
754	90	No data	2023			Livraga	45°11'24.6" 9°31'33.4"	sighting	1
755	91	No data	2023			S. Colombano Lambro	45°11'03.7" 9°30'05.2"	sighting	1
756	92	19/12/2023	2023	12		Castiglione-Camairago	45°12'40.4" 9°42'45.8"	Roadkill	1
757	93	4/2/24	2024	2		Castiglione d'Adda	45°13'05.42" 9°42'45.8"	sighting	
758	94	3/3/24	2024	3		Ospedaletto Lodigiano	45°10'22.12" 9°36'14.88"	Roadkill	1
759	95	23/3/24	2024	3		Caviaga	45°16'18.07" 9°33'55.27"	sighting	1
760	96	7/4/24	2024	4		Casalpusterlengo	45°11'07.89" 9°35'41.21"	sighting	2
761	97	18/4/24	2024			San Fiorano	45°07'56.60" 9°42'40.15"	predation	
762	98	8/4/24	2024	4		Casalpusterlengo	45°12'27.80" 9°35'12.23"	sighting	1



Table I Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf presence (N = 28) and absence ones (N = 35) (Student t-test).

Variables	Presence	Absence	t	P
Poplars	3.5 (0.74)	1.5 (0.22)	2.87	0.006
Meadows	7.1 (1.35)	10.8 (1.31)	1.99	0.051
Scrubland	2.0 (0.27)	1.1 (0.16)	2.96	0.004
Watercourses	2.5 (0.49)	1.3 (0.24)	1.30	0.018

Table II Mean percent values (SE) of the environmental variables with significant differences between municipalities of wolf stable (N = 14) and sporadic (N = 49) presence (Student t-test).

Variables	Stable presence	Sporadic presence	t	P
Arable lands	82.1 (1.72)	62.8 (1.39)	2.05	0.044
Poplars	3.8 (1.17)	2.0 (0.33)	2.08	0.042
Tree crops	1.5 (1.22)	0.1 (0.03)	2.16	0.035
Deciduous woods	2.2 (0.87)	0.9 (0.24)	2.20	0.032
Riparian woods	4.9 (2.05)	2.5 (0.22)	2.10	0.040
Wetlands	0.4 (0.18)	0.1 (0.03)	3.03	0.004
Nature reserve	3.8 (3.13)	0 (0)	2.34	0.023

Table III Results of the GLM on the presence (1) and absence (0) of the wolf in the municipalities of the Lodi province (LCL: Lower Confidence Limit 95%; UCL: Upper Confidence Limit 95%).

Variables	Coefficients	SE	LCL	UCL	Wald	P	Exp(b)	VIF
Meadows	-0.2	0.07	-0.4	-0.1	6.52	0.011	0.83	1.4
Urban areas	-0.5	0.18	-0.9	-0.2	7.98	0.005	0.61	2.0
Urban green areas	2.7	1.17	0.8	5.3	5.14	0.023	15.17	3.2
Roads	-1.1	0.43	-2.0	-0.3	6.29	0.012	0.34	2.0
Wetlands	1.4	1.09	-0.5	3.9	1.75	0.186	4.24	1.2
Intercept	3.4	1.11	1.5	5.9	9.09	0.003	29.01	



Table IV. Results of the GLM on the stable presence (1) and sporadic presence (0) of the wolf in the municipalities of the Lodi province (LCL: Lower Confidence Limit 95%; UCL: Upper Confidence Limit 95%).

Variables	Coefficients	SE	LCL	UCL	Wald	P	Exp(b)	VIF
Wetlands	5.7	1.99	2.40	10.4	8.34	0.004	2.97	1.2
Urban areas	0.2	0.13	-0.01	0.5	2.91	0.088	1.25	2.0
Arable lands	0.3	0.12	0.10	0.6	7.63	0.006	1.41	3.2
Tree crops	2.7	1.00	1.00	5.4	7.36	0.007	1.54	2.0
Poplars	0.5	0.23	0.20	1.1	5.34	0.021	1.69	1.4
Water basins	1.5	0.65	0.20	2.9	4.90	0.027	4.34	1.4
Intercept	-30.5	10.84	-56.50	-13.1	7.87	0.005	<0.0001	

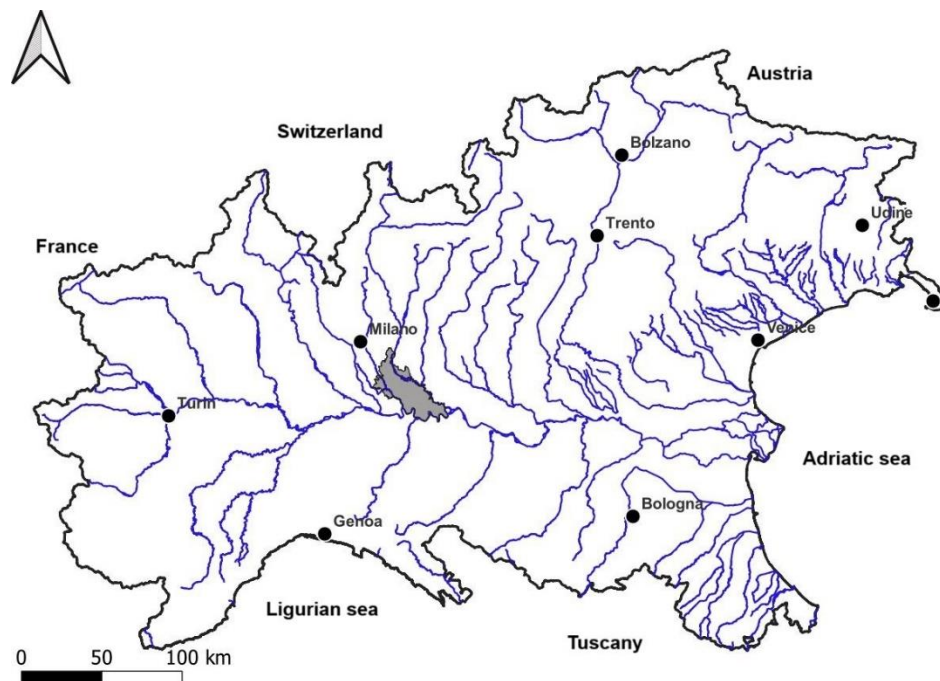


Figure 1. Location of the province of Lodi in Northern Italy (in grey). The main towns and rivers are evidenced.

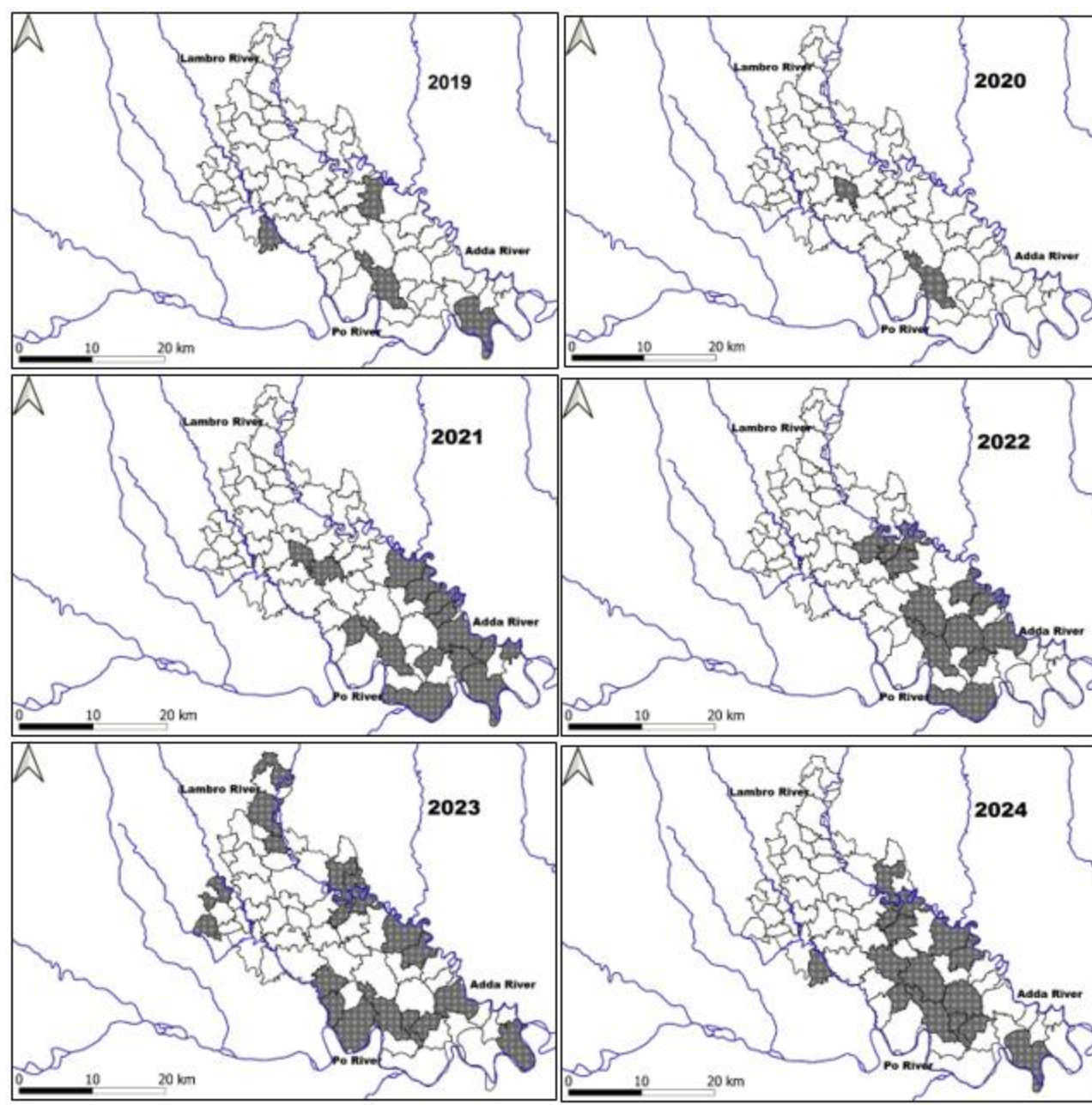


Figure 2. Time scan (2019-2024) of wolf colonization in the Lodi province (N-Italy, Lombardy)

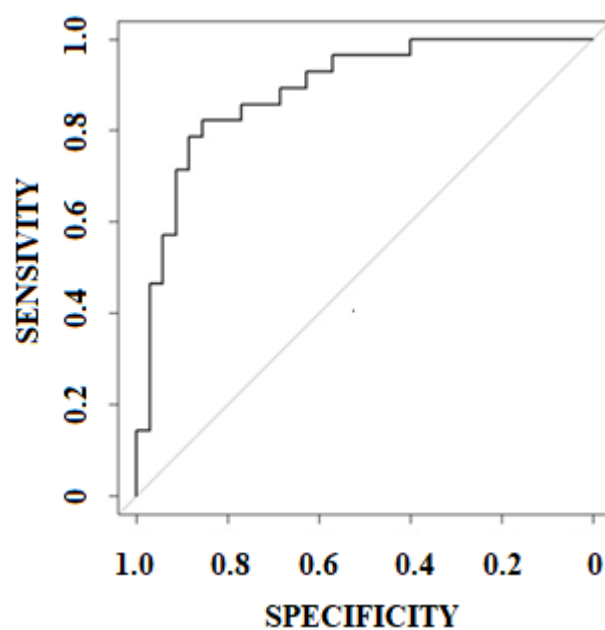


Figure 3. Roc curve of the GLM for wolf presence/absence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly)

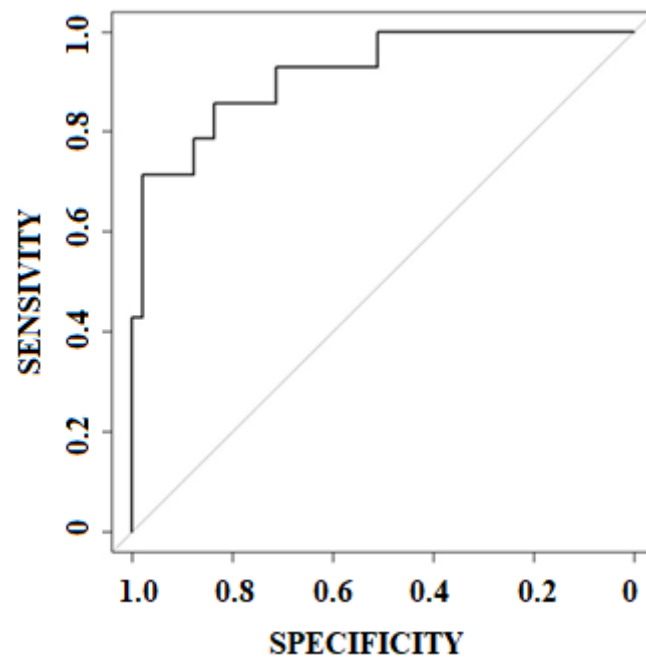


Figure 4. Roc curve of the GLM for wolf stable presence in the municipalities of the Lodi province (the grey line represents the curve of a model that classifies the cases randomly)

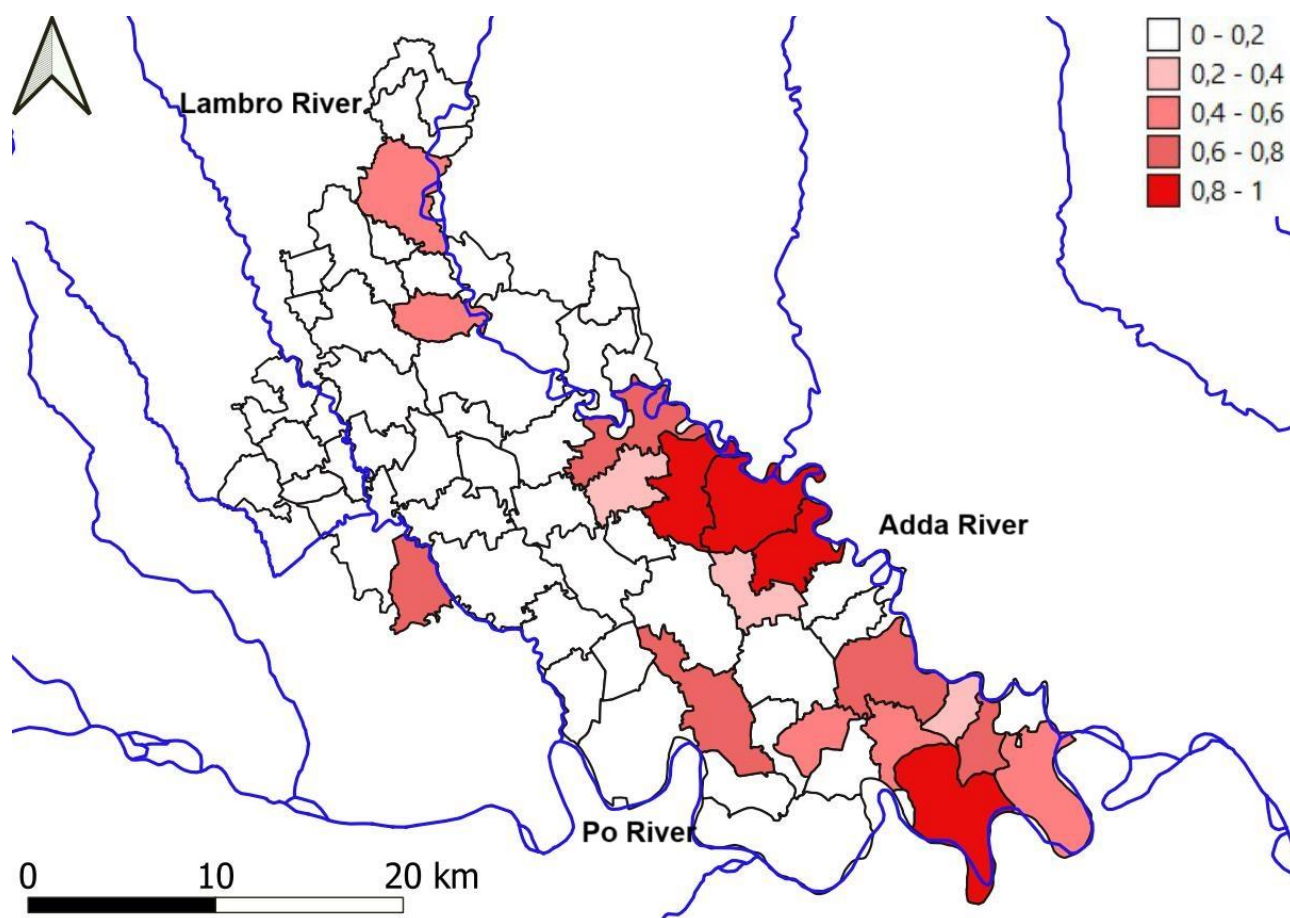


Figure 5.- Stable presence probability map for the wolf in the municipalities of the Lodi province (NW-Italy, Lombardy)



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