Title: Dietary studies provide a partial picture of the feeding ecology of grey wolves across different environments

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Abstract

The recent and ongoing expansion of grey wolves (*Canis lupus*) in Europe has led them into new ecological contexts, including areas characterized by poor prey communities and higher levels of landscape anthropization. While dietary studies are essential for predicting wolf's ecological functions/role and impacts, it remains unclear whether research on wolf diet has kept pace with this expansion, potentially leaving knowledge gaps in newly occupied landscapes.

By using Italy, a country where wolves recovered most of their historical range, as a case study, we mapped the current distribution of wolves and then distinguished between areas with different food resources: domestic or wild ungulates, the coypu (*Myocastor coypus*), and resources associated with landscape anthropization, such as food wast and domestic pets. Finally, we checked the coverage of these areas by dietary studies (n = 36).

The distribution range of wolves in Italy includes areas with nine different food resource assemblages. However, most studies on wolf diet have focused on remote areas of the Alps, where northern chamois and red deer are abundant, and on the Northern and Central Apennines with a rich assemblage of wild ungulates. The feeding ecology of wolves remain largely unexplored in highly anthropized landscapes and in areas of Southern Italy with poorer ungulate assemblages, despite these environments together accounting for most areas of ongoing wolf expansion.

Knowledge gaps about highly anthropized landscapes hinder the role played by rodents, animal byproducts, domestic pets and food waste as resources. And their influence over the fitness of wolves, mediated by their energetic content and predictability, as well as by their capacity to expose wolves to toxic compounds or pathogens. Similarly, knowledge gaps about Mediterranean environments, where wolves rely almost exclusively on wild boar, hinders our ability to predict the potential impact of African Swine Fever on wolf ecology and behaviour.

Carefully evaluating dietary studies about wolves, in their coverage of the different environmental conditions where they live, is crucial to better understand their feeding ecology and role as predators and scavengers, as well as to guide research to address knowledge gaps and predict future changes in their ecology.

Keywords: mammals; diet; predation; large carnivores; feeding ecology; cluster analysis

1. Introduction

The recovery of large carnivores in Europe and North America (Di Bernardi et al., 2025; Ingeman et al., 2022) poses significant questions about their ecological role as predators and scavengers, as well as about their ecological role (Ripple et al., 2014, 2016; Ford and Goheen, 2015).

These questions are particularly relevant in the case of the grey wolf (*Canis lupus*) in Europe. The grey wolf is by far the large carnivore which recovered the most in the last four decades, both in its distribution and numbers. European wolves nowadays inhabit a wide range of environments, which differ in their anthropization, human activities, forest cover, and wildlife communities (Di Bernardi et al., 2025).

The ecological role that wolves can play is therefore likely to be extremely variable, throughout their distribution range. Available evidence indicates that wolves living in Europe, through a range of mechanisms, can change the vigilance behaviour, activity rhythms and space use of large ungulates (Gerber et al., 2024), mesocarnivores (Diserens et al., 2021, 2022; Lazzeri et al., 2024; Selonen et al. 2022) and beavers (Gable et al., 2023 for *Castor canadensis*). Several studies have also investigated the capacity of wolves to regulate demography (van Beeck Calkoen et al., 2023) and spatial distribution of wild ungulates (Bubnicki et al., 2019), mesocarnivores (Krofel et al., 2017) and beavers (Gable et al., 2018). These effects may have cascading consequences on ecosystem processes, including vegetation dynamics (Churski et al., 2021; Gable et al., 2023; Kuijper et al., 2013), hydrological cycles (Gable et al., 2023), and carrion availability in the environment (Brogi et al., 2025).

Research synthesis (Gurevitch et al., 2018) is particularly important to draw conclusions about the potential existence and magnitude of these trophic cascades, and different reviews and meta-analysis covered this topic (see, Gerber et al., 2024, Kuijper et al., 2016, 2024 and van Beeck Calkoen et al., 2023 for Europe; see, Ripple et al., 2014 for a global perspective). However, the rapid and widespread expansion of wolves in Europe, coupled with the fact that trophic cascades are strongly context dependent and mediated by local ecological conditions and human presence (Haswell et al., 2017), raises the question on whether existing literature is truly capturing the different environmental conditions characterizing the distribution range of wolves. For example, Gerber et al. (2024) found that most European studies about ungulate responses to wolves, and their ecological effects, come from few geographical regions with a low human impact, whereas most Europe includes landscapes with a rather high level of anthropization. This conclusion was also drawn by Kuijper et al. (2024), who also suggested that the current expansion of wolves into human-modified ecosystems, where they were had been absent for centuries, could result into new and context-dependent ecological interactions.

Identifying gaps in existing research is therefore particularly useful to put in perspective findings about the ecological effects of wolf return and, most importantly, to guide new studies aimed at filling these gaps. Given the direct relationship between wolf's feeding habits and its ecological function, this is particularly urgent for research about wolf diet (Newsome et al., 2016).

Although various authors have emphasized the behavioural effects of wolves on other species, predation itself can exert substantial ecological impacts, particularly in areas with low human presence and ecologically functional densities of wolves (Kuijper et al., 2016). In addition to their role as apex predators, wolves significantly influence scavenging dynamics, both as carcass producers (through kills and incomplete consumption, Brogi et al., 2025) and as scavengers themselves, feeding on remains from other predators or human activities (Wirsing and Newsome, 2021). Studying the diet of wolves therefore provides critical insight into the pathways through which wolves shape ecosystems through direct predation, induced behavioural modifications, and scavenging. This knowledge can therefore inform ecological models aimed at predicting the magnitude and temporal evolution of these effects (Passoni et al., 2024). A sounder understanding of the diet of wolves, throughout their range, would also allow to better understand how human activities (e.g., hunting, herding, waste disposal), emerging diseases (e.g. African Swine Fever;

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hereinafter ASF, EFSA 2024), or climate change, can moderate the current and future ecological impact of wolves in Europe, by acting on their food sources.

However, since different parts of the wolf's range offer highly variable food resources due to the distinct spatial distributions of prey species (e.g., ungulates, ENETWILD-consortium 2022; e.g., the Eurasian beaver, *Castor fiber*, Gable et al., 2018) it is essential to assess how well the spatial distribution of wolf diet studies aligns with the distribution of the available prey assemblages. In this study we used a data-based approach to categorize the distribution range of wolves in Italy in terms of the main food resources available to wolves and to quantify the extent to which different ecological conditions have been covered by dietary studies. Italy is among the European countries that, since the 1970s, had the most marked increase in wolves (Di Bernardi et al., 2025; Zanni et al., 2023). Starting from a small population of a few hundred individuals in remote areas of Central Italy at least 2,945 – 3,608 individuals are nowadays thought to be present (La Morgia et al., 2022). The surprising speed of wolf expansion in Italy, leading to the recovery of most of its historical range, makes it a perfect workbench to highlight potential spatial biases in wolf diet literature and guide further research.

Our approach indicates that the current distribution range of wolves includes areas with a different availability of food sources, corresponding to 4 overall environmental conditions. However, knowledge gaps still characterize the diet of wolves in anthropized landscapes and in areas where they rely on an incomplete assemblage of wild ungulates.

2. Materials and methods

2.1. Collection of studies and inclusion criteria

Data collection adopted a threefold approach. First, we extracted all those studies that were mentioned in reviews about wolf diet (Janeiro-Otero et al., 2020; Meriggi et al., 2011; Mori et al., 2017; Newsome et al., 2016; Zlatanova et al., 2014), and that were conducted in Italy between 2007 and 2023.

Moreover, we also searched for the keywords "*Canis lupus*", "*wolf*" and "*diet*" (similarly to Newsome et al., 2016) on three large datasets of scientific publications: Scopus, Web of Science, and Google Scholar. Then, from this second pool of studies, we selected those which had been carried out in Italy and were published between 2007 and 2023. As the period when data had been collected was not always reported, and results were often not split between different years, we used the year of publication to assign each study to one of the following periods: 2007-2012, 2013-2018, and 2019-2024. We also retrieved studies that were carried out after the most recent review about wolf diet (Janeiro-Otero et al., 2020), or that had been discarded by previous reviews. Finally, we also collected available grey literature about wolf diet in Italy. This included non-peer reviewed documents, such as dissertations of MSc and PhD students that had not been subsequently published in a peer-reviewed journal, or reports published by local and protected areas' authorities. As dissertations are not always adequately indexed on the archives of Italian universities, we used snowballing. First, we queried "*Dieta lupo*", the Italian translation of "*Wolf diet*" on university archives and Google. Then, we also asked other researchers and practitioners, working on wolf conservation and ecology, about further grey literature on wolf diet that we could have missed. From the pool of studies that we had obtained, we retained those for which it was possible to understand where data had been collected, with respect to the grid used by the Ministry for the Environment to quantify wolf occupancy in 2019-2021 (La Morgia et al., 2022).

Although different methods for investigating wolf diet may provide different results (Klare et al., 2011), we did not discard studies according to the method they used as our meta-analysis focused on assessing spatial bias. So, we pooled together studies relying on scat analysis, barcoding, stomach contents and isotopes.

2.2. Quantification of spatial location, measurements and statistical analysis

We used a 10-km resolution grid produced by the Ministry of the Environment (La Morgia et al., 2022) and by Wolf Alpine Group (2024) to identify the distribution range of wolves in peninsular Italy, until early 2024. We also downloaded distribution maps for 2007-2012 and 2013-2018 from reports of the Habitat Directive (http://reportingdirettivahabitat.isprambiente.it/) and calculated areas where wolves have expanded, during the 2019-2024 period (Fig. 1).

Then, for each cell of the grid we extracted variables related to the main food sources available to wolves. These included: anthropization and the presence of domestic livestock, wild ungulates, and the coypu (*Myocastor coypus*).

Anthropization affects wolf diet mostly through food waste, which is a nearly unlimited food source. Although wolves do not fully exploit carbohydrates (Axelsson et al., 2013), evidence from non-European countries indicate that they exploit food waste whenever available (Barocas et al., 2018; Mohammadi et al., 2019), probably by selecting for meat scraps and bones. Moreover, wolves living around human settlements could also prey on pets (Bassi et al., 2021; Kojola et al., 2022; Nowak et al., 2011). We quantified anthropization by calculating evenness of human density, quantified at a 1km resolution through the Global Human Settlement Layer (https://human-settlement.emergency.copernicus.eu/index.php), for each cell of our grid. Evenness was quantified through the Gini index, which varies from 0, when all the units of a sample have the same value of a certain measure, to 1 when one unit has the entire amount of that value. Therefore, the Gini index was positively associated with the amount of natural landscapes in each cell, with cells having the lowest values being characterized by widespread human settlements and having therefore a higher availability of food waste and domestic pets.

We also considered the abundance of domestic livestock, particularly sheep, cattle, and domestic pigs, that can be regularly preyed on by wolves (Gervasi et al., 2021). Moreover, the abundance of livestock could also account for the availability of carrion and slaughterhouse remains in the environment, important supplementary food sources for wolves (Ciucci et al., 2020; Ćirović and Penezić, 2019). For domestic livestock, we used 10 km abundance projections generated by the Food and Agriculture Organization and structured in the Gridded Livestock of the World database (GLW4, https://data.apps.fao.org/catalog/dataset/15f8c56c-5499-45d5-bd89-59ef6c026704), related to the abundance of sheep, cattle, and domestic pigs. Indeed, densities of domestic livestock had a different meaning for different livestock species. Although sheep in Italy are almost entirely raised extensively, cattle and pigs have profound differences in their husbandry type, with lowlands in Northern Italy being characterized by intensive livestock farming, which alone accounts for 30 % of the total cattle and 88% of the total pigs raised in the country (https://www.vetinfo.it/j6_statistiche/#/). Areas with a high density of cattle and pigs therefore correspond to areas with intensive livestock farming, where animals are kept in the barn and are thus not available for wolves when alive, but where wolves can feed on byproducts (e.g. placentae) and slaughtering leftovers.

For wild ungulates, we considered the five most preyed on by wolves in Italy: roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and Northern chamois (*Rupicapra rupicapra*) (Gazzola et al., 2007, Mattioli et al., 2011; Torretta et al., 2018). We did not consider the mouflon (*Ovis gmelini musimon*), which is distributed with scattered populations in the Italian peninsula, although occasionally it could represent an important prey (Capitani et al., 2004). Moreover, we did not consider the Sika deer (*Cervus nippon*), because its distribution in Central and Northern Italy is still uncertain (Mori et al., 2024). Neither we considered the Alpine ibex (*Capra ibex*), as it seems to play a minor role in the diet of alpine wolves (Palmegiani et al., 2013), nor did the Apennine chamois (*R. pyrenaica ornata*), due to its limited distribution and the small size of its populations (Corlatti et al., 2022). For wild ungulates, we relied on 10-km hunting yield density maps elaborated within the ENETWILD project

(ENETWILD consortium et al., 2022), using them as relative indexes for the local abundance of each wild ungulate species.

Finally, we also included the potential environmental suitability of the Italian peninsula for the coypu. Recent studies found out that the coypu can be an important prey, in some agricultural ecosystems of Central and Northern Italy (Musto et al., 2024; Ferretti et al., 2019; Marras and Marucco, 2022), probably because it is easy to prey and can attain very high densities, providing wolves with a relevant biomass (Balestrieri et al., 2016). As no abundance map was available for this species, we rather used the potential suitability of the Italian landscape, at a 1 km resolution, obtained from Schertler et al., (2020). For each cell of our grid, we calculated the median for the abundance of wild ungulates and livestock and the geometric mean for the suitability for the coypus. Although wolves in many areas of Central and Northern Europe regularly prey on other aquatic rodents, such as the Eurasian beaver (Gable et al., 2018), we did not include this species, because its population in Central and Northern Italy is still extremely small and confined to few areas (Bertolino et al., 2023).

Indeed, both ENETWILD maps and the map from Schertler et al. (2020), have their values spanning beyond the actual distribution range of the different species. Therefore, we used data from the Italian Atlas of Mammals (Loy et al., 2025), to crop these maps with respect to the effective distribution range of the different species that we considered. See Appendix 1 for a complete overview of the different variables used to identify different ecological conditions.

We identified food resources assemblages as homogeneous areas within the entire Italian peninsula, based on: *i*) the Gini index of human density, *ii*) the median abundance of roe deer, red deer, wild boar, fallow deer and Northern chamois, *iii*) the median abundance of domestic pigs, sheep and cattle, i*v*) the geometric mean of the potential suitability for the coypu. To this end, we used the CLARA algorithm, an extension of Partitioning Around Medoids cluster analysis. We chose the CLARA algorithm due to the high number of cells (n = 2,510) and its robustness against non-normal data and outliers. The number of clusters was chosen by graphically exploring the silhouette width method, the elbow method, and the gap statistics method (Kassambara, 2017). Before clustering our cells, we standardized and centred our variables. Due to missing values in the raster showing the distribution of food sources, we could categorize only 89.3% of the total Italian peninsula. Almost all the cells that we did not categorize occurred in coastal areas (Fig. S4 in Appendix 1).

Then, we assigned each selected study to the various cells of the grid. Based on the information included in the analysed studies about the geographical position of their study areas, we identified the location of each study as the geographical centre of the area where biological samples had been collected. Then, we assumed that wolves for which biological samples had been collected on the centroid, could have moved in a home range of approximately 113 km^2 (Mancinelli et al., 2018; Mattioli et al., 2018) and so we generated a buffer with a radius of 6 km around each point and classified all those cells of the grid that overlapped with it. As our scope was to assess the spatial coverage of existing studies about wolf diet, and because many studies refer to the same research project, we only classified the cells of our grid as being covered by studies or not, with a dichotomous variable.

Once we identified environmental clusters, we graphically inspected how studies about wolf diet were distributed between different clusters in the 2007-2024 period, although we clusterised environmental variables in the entire Italian peninsula, we then only explored coverage in those cells that corresponded to distribution range of the wolf in early 2024 (n. cells = 2,510). We calculated both *i*) the portion of dietary studies being conducted in each different cluster and *ii*) the portion of cells of each cluster being involved in at least a dietary study. Statistical analyses were carried out in R (R Core Team 2023).

3. Results

Our final dataset included 36 studies (Appendix 2): 27 of them were published in peer-reviewed journals, 8 of them were MSc dissertations and 1 was a study published in the proceedings of a scientific conference. The number of dietary studies increased across the three study periods, with 8, 13, and 15 studies being published in the periods 2007-2012, 2013-2018, and 2019-2024, respectively.

Cluster analysis identified 9 food resource assemblages, each one categorized by a different availability of prey and other food resources (Fig. 2, see Appendix 3 for a detailed description). On the basis of their geographic distribution and ecological profile, these 9 assemblages may be grouped into 4 broader environmental types: *i*) areas of the Alps with a low landscape anthropization and the presence of the northern chamois, the roe deer and the red deer (ALA), *ii*) areas with a rich assemblage of wild ungulates, characterized by high densities of red deer, roe deer, fallow deer and wild boar (RAW), *iii*) areas with an incomplete assemblage of wild ungulates, where one or more species are missing (IAW) and *iv*) areas with a medium-to-high level of landscape anthropization (HAL).

When checking the difference between the percentage of cells that were covered by studies and the percentage of cells from each food resource assemblage cluster within the distribution range of wolves (Fig. 3, Table 1), two points emerged. First, areas of the Alps with a low landscape anthropization and areas with a rich assemblage of wild ungulates had a positive difference, revealing that more studies had been carried out in these two environments, than expected from a homogeneous distribution of studies in the wolf range. Conversely, areas with an incomplete assemblage of wild ungulates and areas with a medium-to-high level of landscape anthropization were proportionally less covered by dietary studies (Fig. 3).

Among areas with an incomplete assemblage of wild ungulates, dietary study coverage was particularly low for those areas where the only abundant wild ungulate is the wild boar, which are widespread in Southern Italy, and areas with abundant wild boar and roe deer, in Central Italy.

Among areas with anthropized landscapes, forest coverage was extremely low for highly anthropized areas, which were also characterized by a substantial availability of coypu. Finally, although areas of Northern Italy with intensive livestock farming account only for a very small fraction of the distribution range of wolves (0.9%), no study has ever explored the diet of this species in this environment.

4. Discussion

The grey wolf has been steadily expanding its distribution range in Italy, since the 1970s, recovering most of its historical distribution and probably having now complex ecological interactions in a wide range of different ecosystems. However, our findings highlight that existing research about wolf diet is characterized by knowledge gaps, deriving from spatial biases (Hughes et al. 2021) that prevent to understand and predict these ecological interactions and their future evolution. In the following lines we will discuss our findings about the different degrees of wolf dietary study coverage across the four major environmental types that emerged from our data analysis.

41. The grey wolf's diet in areas of the Alps with a low landscape anthropization

Approximately 5.9% of the distribution range of wolves in Italy occurs in areas of the Alps, characterized by a low landscape anthropization and with few human settlements, mostly limited to villages located in valley bottoms. These areas, mostly located in the northwestern, southwestern and northeastern sectors of the Alps (Fig. 2), were interested by a substantial dietary study coverage (Fig. 3, Table 1).

Due to the low level of landscape anthropization, and the resulting small amount of food waste and domestic pets associated with high densities of northern chamois and intermediate densities of red and roe deer, wolves in these environments rely on wild ungulates (Capitani et al., 2004; Gazzola et al., 2007; Marucco et al., 2008; Meriggi et al., 2011; Palmegiani et al., 2013; Torretta et al., 2017). Wolves also feed on livestock grazing on high-elevation pastures during summer, particularly when these are not adequately protected through fences and guarding dogs (Gervasi et al., 2021; Menzano et al., 2023; Selva et al., 2023).

Although these environments are not those with the largest knowledge gaps, future studies could still shed light on aspects of the feeding ecology of wolves which are relevant for the conservation of other species and for the Alpine ecosystem structures. For example, due to climate change, cold adapted ungulates such as the northern chamois (Mason et al., 2014; Corlatti et al., 2022; Malagnino et al., 2024; Thel et al., 2024) or the alpine ibex (Brivio et al., 2019, 2024; Semenzato et al., 2021) will most likely change the spatio-temporal patterns of their behaviour. As a consequence, even though wolves in the Alps mainly prey on deer species (but see Palmegiani et al., 2011), it was highlighted that climate change-driven increased nocturnality of alpine bovids may increase their likelihood of being predated by wolves in the near future (Brivio et al., 2024). At the same time, climate change forcing uphill movements (Butghen et al., 2017) are expected to reshape the use of key foraging habitats, namely grasslands (Masoero et al., 2024) and forests (Reiner et al., 2021, 2022), by alpine ungulates. These shifts may alter the relative susceptibility to wolf predation of bovids and red deer, a species with major ecological impacts on structure and functioning of alpine grasslands and forests, whose increase could affect the cycle of nutrients (Riesch et al., 2022) and biotic communities (Gobbi et al., 2018; Iravani et al., 2011; Schütz et al., 2003).

4.2. The grey wolf’s diet in areas with a rich assemblage of wild ungulates

A significant part of the distribution range of wolves (9.2%) includes areas with a low level of anthropization, where they can rely on the three most widespread deer species (red, roe, and fallow deer) as well as on the wild boar. These areas are concentrated mostly on the northern sectors of the Apennines, with a few isolated nuclei in the Alps and Southern Italy (Fig. 4).

These areas have been largely covered by existing studies, with 22.9% of their cells having been included in diet study areas, therefore they are not characterized by significant knowledge gaps (Fig. 3). However, a major characteristic of wolf diet in these areas is the prevalence of wild boar, which is the main prey across all Northern and Central Apennines (Mattioli et al., 2011; Meriggi et al., 2011). As in the next few years the populations of wild boar in the Italian peninsula will likely be abruptly reduced by ASF, these assemblages will likely be destabilized, and future studies should explore the potential adaptation of wolves to reduced abundances of the wild boar (see Section 4.3 for a more detailed discussion).

4.3. The grey wolf in areas with an incomplete assemblage of wild ungulates

Most of the range of the grey wolf in Italy (67.8%) is nowadays characterized by environmental conditions where wolves inhabit landscapes with a low degree of anthropization and abundant wild ungulates. However, assemblages of wild ungulates are highly variable with one, or more, species that are systematically missing. Most of these areas have food resource assemblages with the wild boar as the only abundant ungulate, or the wild boar and the roe deer, and lack the fallow and/or the red deer (Fig. 5).

Decades ago, most landscapes in these areas where inhabited and cultivated, then socioeconomic changes led to their progressive depopulation (Viesti, 2021), with a loss of agricultural areas and a strong increase in the coverage and complexity of forests (Agnoletti et al., 2018). Because all these large-scale dynamics are relatively recent, these areas are extremely interesting from an ecological viewpoint. In fact, it is well known that differences between assemblages of large ungulates, in terms of number of species and abundance, influence the structure and dynamics of forests, as well as the local soil and biotic communities (Bernes et al., 2018; Ramirez et al., 2018, 2021; Suzuki, 2024). Studying the diet of wolves in these environments would therefore allow us to understand their ecological role as predators in a highly dynamic context, where the selection of wild ungulates can have strong ecological effects on the vegetation and the soil. These effects are also likely to be rapid, considering the current size of wolf population in Italy (2,945 – 3,608 individuals, see La Morgia et al., 2022) and the most recent estimates of predation rates (Bassi et al., 2020). Moreover, studying the diet of wolves in these environments would also allow us to understand the ecological implications of prey shifting. For example, Lazzeri et al. (2024) found that in an area of Central Italy wolves rapidly switched from a diet mostly relying on the fallow deer, which impacts the vegetation through grazing and browsing (Esattore et al., 2022), to the wild boar, whose ecological impacts are mediated by soil rooting and omnivory (Barrios-García et al., 2012).

Unfortunately, despite their extension and ecological importance, the environmental type where wolves could prey on incomplete assemblages of wild ungulates has not been adequately covered by dietary studies (Fig. 3), with two types of areas being particularly ignored.

The first one includes those areas, mostly in Central and Southern Italy, where the wild boar is by far the most abundant wild ungulate. These include 25.5% of the current wolf distribution range and 30.3% of those areas where wolves have expanded after 2018. Considering that Italy is currently facing an outbreak of ASF (EFSA, 2024), with some confirmed cases in Southern Italy (Pavone et al., 2023), the consequences of ASF expansion can be more substantial than for areas with complete assemblages of ungulates (see section 4.2). Long-term dietary studies are needed to understand the extent to which wolves could shift to other wild ungulates or domestic animals. This process has been studied in other areas of Central Europe, affected by ASF (Klich et al., 2021 a,b; Valdmann and Saarma 2020), but no study has been carried out in the Mediterranean region. As wolves might shift to domestic animals, such as pets or livestock (Klich et al., 2021a), sometimes with a considerable degree of spatial variation caused by pack-specific behaviour (Ciucci et al., 2018, Jędrzejewski et al., 2012), this knowledge will ultimately contribute to forecast areas where ASF can trigger human-wolf conflicts.

The second context includes areas where the wild boar and the roe deer are the only abundant wild ungulates. These are also concentrated mostly in Central and Southern Italy (23.4 % of the distribution range) and are not adequately covered by dietary studies (Fig. 3). As these areas are also facing ASF, and as wolf is a species which can change the main prey item according to density fluctuations of available wild prey (Davis et al., 2012), it would be useful to understand the extent to which wolves could shift to roe deer, a browser that sometimes has strong impacts on the vegetation (Hardalau et al., 2024) and that in last decades is decreasing in some areas of Europe, due to landscape and/or climate change (Apollonio and Chirichella 2023).

4.4. The grey wolf's diet in anthropized landscapes

Nowadays, 17.2% of the distribution range of wolves, and 31.9% of areas that were colonized in 2019-2024, is made of three different food resource assemblages, all being associated to various degrees of landscape anthropization. These include rural areas with intermediate levels of landscape anthropization and sheep herding, areas with high landscape anthropization and extremely suitable for the coypu, as well as districts of the Po Plain with medium-high levels of landscape anthropization and intensive livestock farming (Fig. 6). Apart from rural areas with sheep herding, the other two food resource assemblages have been extremely understudied. We believe that attaining a deeper understanding of wolf diet in areas where they live alongside with humans is a priority, to better appreciate their ecological role in a context with major challenges for their conservation (Musto et al., 2021).

In highly anthropized landscapes wolves can access a significant amount of food waste, whose ecological role is probably non-negligible. In Italy, food leftovers accounts for approx. 3.8% of total waste, which in 2023 was estimated at 29 million tons (ISPRA, 2024). Although most of this waste is not accessible to wolves, even a tiny fraction of it would correspond to a very high amount of food. Zlatanova and collegues (2014) have already observed the importance of garbage food in the diet of those wolf population living in anthropogenic habitats, thus assessing the role played by human waste in the diet of wolves living in anthropized environments of northern and central Italy is therefore potentially important to understand their recent expansion in these areas (Zanni et al., 2023). At the same time, there is a need to explore differences between the diet of wolf and wolf-dog hybrids living in these areas. Some dog breeds have alpha amylase, which facilitate the metabolism of carbohydrates (Axelsson et al., 2013); this trait can thus be inherited by wolf-dog hybrids which, in an environment where starch-rich wastes are largely available, could increase their fitness. Finally, studying the consumption of food waste by wolves would be useful to assess their potential exposure to toxic compounds, such as microplastics (Prata et al., 2023) or rodenticides (Musto et al., 2024).

With widespread human settlements, highly anthropized landscapes of northern and central Italy are also rich in terms of domestic pets, such as cats or dogs. Empirical evidence, obtained from the stomach contents of wolves that were found in northern Italy (see Appendix 4) indicates that wolves can prey on domestic pets, particularly cats. Considering that domestic cats and dogs have major impacts on wildlife populations (Doherty et al., 2017; Loss et al., 2022, Bateman and Gilson, 2025), understanding the extent to which wolves prey on these two species will be useful to appreciate their ecological role in anthropized landscapes (Kuijper et al., 2024).

Understanding the consumption of domestic cats and dogs by wolves is also crucial, considering their many shared pathogens (Lescureux and Linnell, 2014). For example, predation on cats can expose wolves to toxoplasmosis, with potential changes in their behaviour (Meyer et al., 2022) and ecological effects. Not forgetting the effect of pet consumption by wolves on public opinion, possibly leading to a change of attitude towards the species in urban areas.

Anthropized landscapes of central and northern Italy are also highly suitable for the presence of the coypu. Existing studies indicate that the coypu can be an important prey for wolves (Ferretti et al., 2019; Marras and Marucco, 2022). Considering that the coypu is an invasive alien species, which negatively affects ecosystems in its invaded range by altering the soil, water quality and vegetation (De Michelis et al., 2024; Sofia et al., 2016), studying the diet of wolves in anthropized landscapes will be useful also to evaluate their ecological role as predators of a widespread invasive ecological engineer.

Finally, it is worth noticing that the diet of wolves has never been studied in those areas of the Po Plain, where the species lives in districts of intensive livestock husbandry. Although these areas are a minority of the distribution range of the species (0.9%), and despite it is unclear the ecological role that wolves can play there, we believe that understanding their diet in these conditions is valuable, from a conservation viewpoint. Namely, if wolves feed on slaughtering leftovers, as well as on other byproducts (e.g., placentae of cattle, carrion, Ciucci et al., 2020), they can be exposed to a wide range of pathogens, including antibiotic-resistant bacteria (Dolejska et al., 2020).

4.5. Limitations of this study

Although our findings are useful to identify knowledge gaps and guide new research about the diet of wolves, it is important to emphasize that this study also has some limitations.

First, we only considered studies that had been carried out in Italy. Although wolves in Europe inhabit a wider range of environments than in Italy (Di Bernardi et al., 2025), this country constitutes a valuable case study to show how the distribution of dietary studies influences our understanding of the feeding ecology of wolves, due to the fact that wolves recovered most of their historical range and dietary studies were particularly abundant. Moreover, by focusing on a single country we were able to retrieve a significant amount of grey literature. Nevertheless we believe that future studies should scale up our approach to larger spatial scales.

Moreover, in our study we used model-based predictions of the abundances of the wild ungulates obtained from hunting bag. While hunting bags can differ from the real density of animals in the environment (Imperio et al. 2010), our data had been calibrated and were found to capture large-scale gradients in the abundance of large ungulates (ENETWILD-consortium et al., 2022). The predicted environmental suitability for the coypu, which was high for northern Italy (see Appendix 1), also aligns with trends in the abundance of this species, which in the Po Plain is subjected to intensive culling, with thousands of individuals killed every year (Bertolino et al., 2012).

We are also perfectly aware that wolves are extremely flexible in their diet, which goes far beyond the prey species that we considered (Newsome et al., 2016). Nevertheless, we believe that our findings can still be useful to address gaps in the diet of wolves, in a way that can be useful to understand and predict their ecological role as predators or scavengers in different ecosystems.

Another major limit of this study is the use of landscape anthropization as a proxy for the availability of food waste. While food waste strongly correlates with human density, we acknowledge that the real amount of undisposed food waste could strongly vary in space and time, based on differences between local public administrations (Pasotti et al., 2010). Although extremely demanding, it would be incredibly valuable to have futures studies coupling the selection of food waste by wolves with its quantification in the environment, through field surveys.

5. Conclusions

Wolves have rapidly expanded their range across Europe and continue to do so, yet research on their dietary habits has struggled to keep pace. As a result, little is known about wolf diet in newly colonized areas, despite their likely environmental differences from long-established populations. These gaps are particularly important given that the environmental conditions of these newly colonized areas may lead to novel wolf's ecological roles (Kuijper et al., 2024), with potential major consequences for ecosystem dynamics and human-wolf interactions. Addressing these gaps should be a priority for future research, ensuring that dietary studies encompass the full range of environmental contexts in which wolves persist. This will provide critical insights into their ecological role, particularly in human-dominated landscapes and in abandoned rural areas where they may influence large-scale ecological dynamics. The urgency of filling this knowledge gap is further heightened by the potential decline in wild boar populations due to African Swine Fever, which could have cascading effects on wolf ecology and human-wolf interactions.

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Conflict of Interest

The author declare no conflict of interest.

Author contributions

Conceptualization: JC, RB, CM, EB **Methodology:** JC, RB, CM, EB **Software:** JC **Validation:** JC, RB, CM, EB, GV, AB, MD, MS, MA **Formal analysis:** JC **Investigation:** JC, RB, CM, EB, GV, AB **Resources:** GV, AB, MD, MS, MA **Data curation:** CM, EB, GV, AB **Writing - original draft:** JC, RB, CM, EB **Writing- review and editing:** JC, RB, CM, EB, GV, AB, MD, MS, MA **Visualization:** JC, RB, CM, EB **Supervision:** MD, MS, MA **Project administration:** MD, MA **Funding Acquisition:** GV, AB, MD, MS, MA

Data availability statement

The reproducible data and software code, are available at: https://osf.io/76cx4/

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Figures

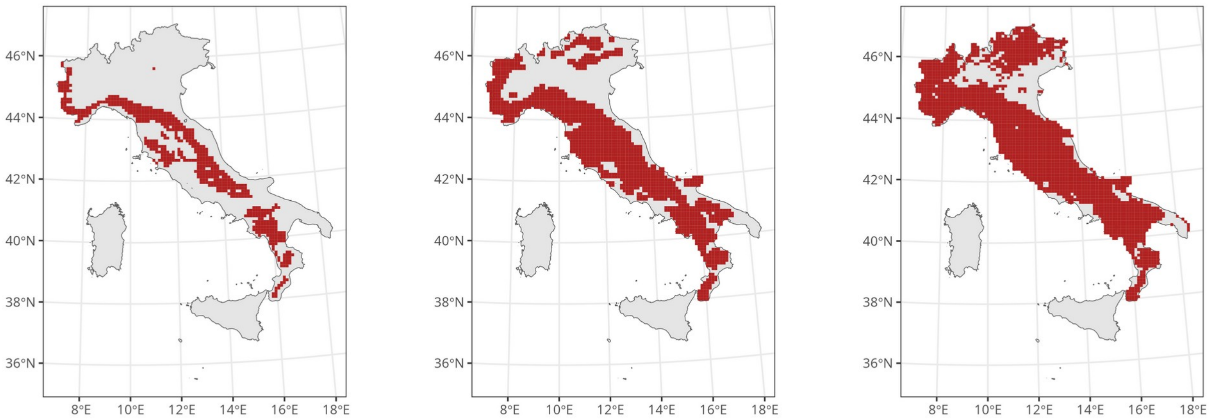

Fig. 1. Distribution of wolves in Italy in 2007-2012 (left), 2013-2018 (center) and 2019-2024 (right). For data sources please see the Methods section.

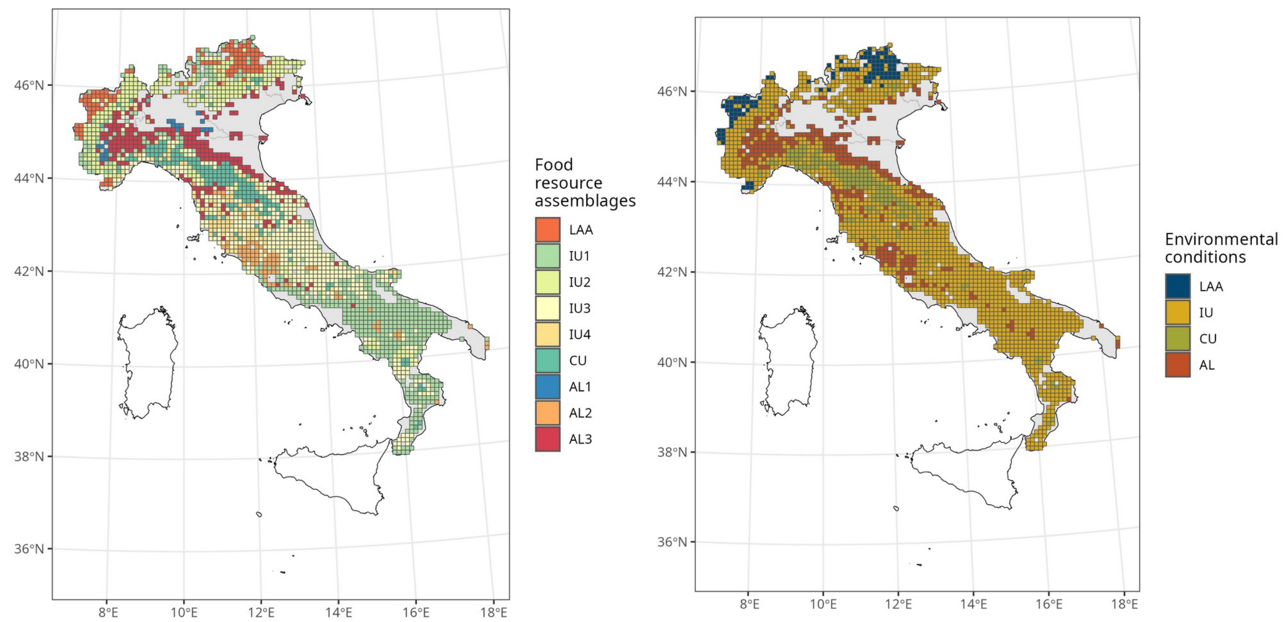

Fig. 2. Spatial distribution, in 2024, of areas with different food resource assemblages (right) and of different environmental conditions (right). Namely low-anthropization areas in the Alps (LAA), areas with an incomplete assemblage of wild ungulates (IU1, IU2, IU3, IU4), areas with a complete assemblage of large ungulates (CU) and anthropized landscapes (AL1, AL2, AL3).

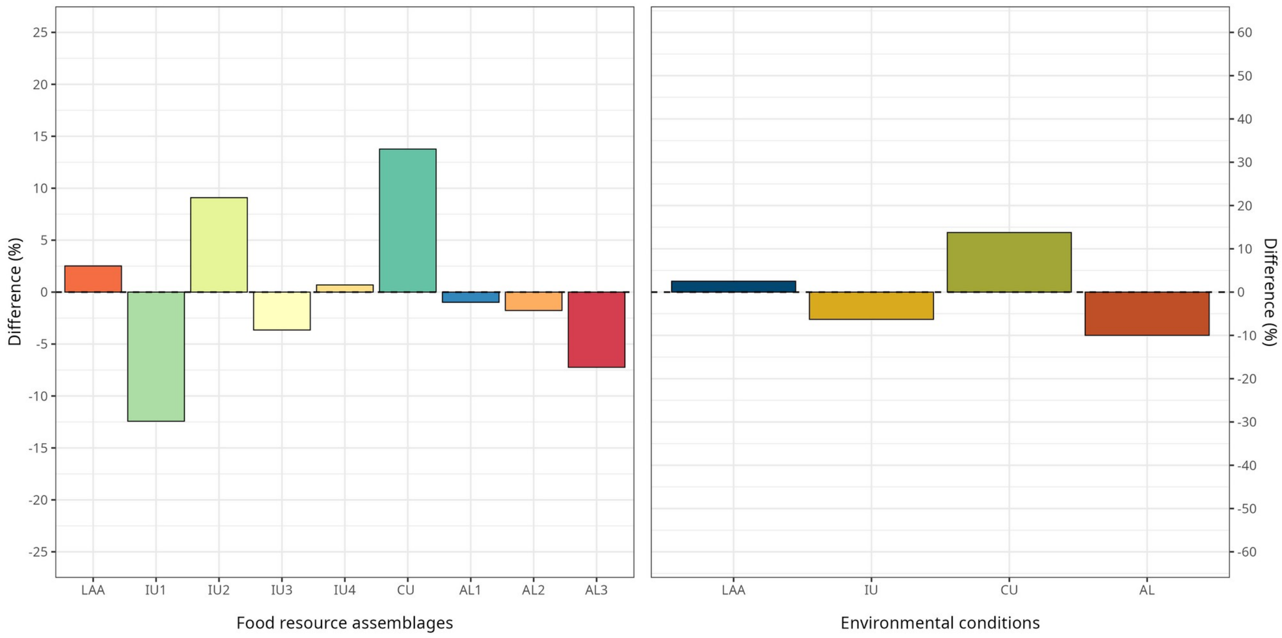

Fig. 3. Difference between the percentage of cells in the distribution range of wolves in 2024 and the percentage of cells that were covered by dietary studies, in each one of the 9 areas with different food resource assemblages (left) and in each of the 4 environmental conditions (right).

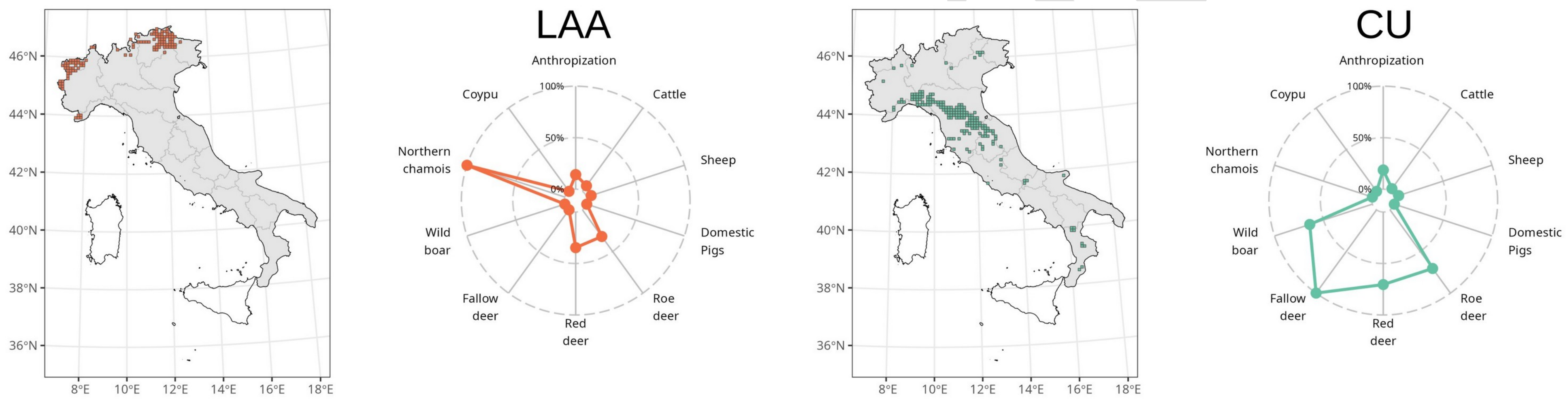

Fig. 4. Distribution of areas with a low landscape anthropization in the Alps (LAA) and of areas with a complete assemblage of wild ungulates (CU), within the distribution range of wolves in 2024. Values within the radar plot correspond to the median value of each variable, between cells from a certain cluster.

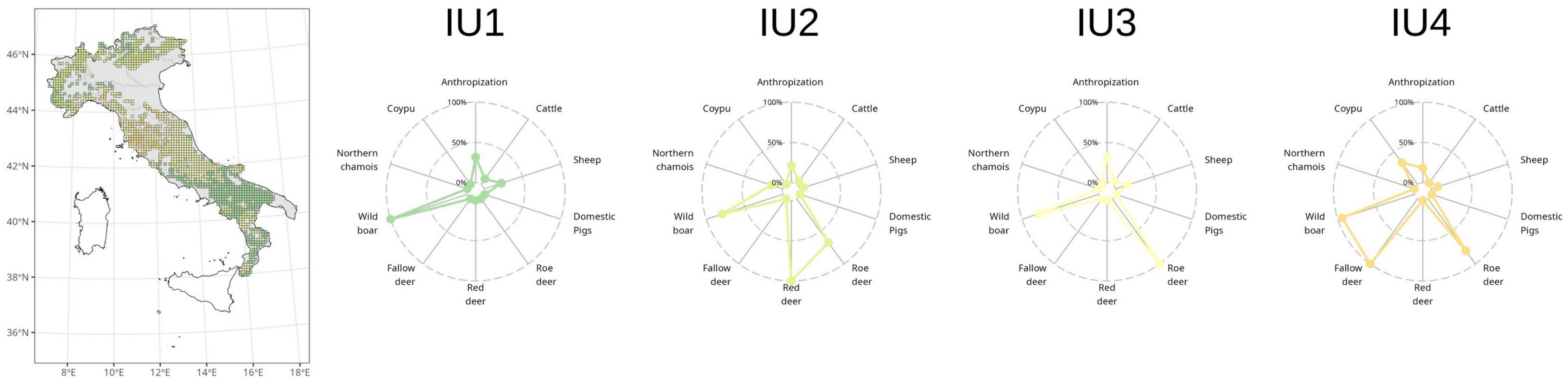

Fig. 5. Distribution of areas with an incomplete assemblage of wild ungulates (cluster IU1, IU2, IU3, IU4), within the distribution range of wolves in 2024. Values within the radar plot correspond to the median value of each variable, between cells from a certain cluster.

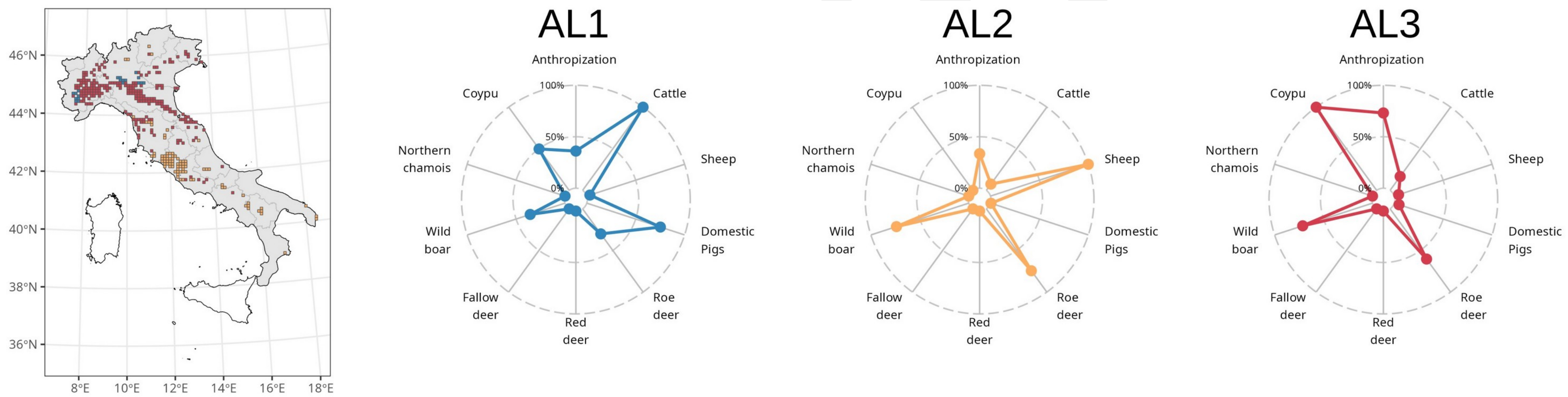

Fig. 6. Distribution of areas with an anthropized landscapes (AL1, AL2, AL3), within the distribution range of wolves in 2024. Values within the radar plot correspond to the median value of each variable, between cells from a certain cluster.

Table 1. Percentage of the distribution range of wolves and the expansion range of wolves (area of presence in 2019-2024 where wolves were not present in 2013-2018), as well as percentage of cells covered by studies about wolf diet, in areas with different food resources and in different environmental conditions.

Areas with different food resources				
Area	% in the distribution range	% in the expansion range	% of the range covered by studies	Difference between % of covered and total cells
LAA	5.8	8.6	8.3	+ 2.5 %
IU1	25.5	30.3	13.0	- 12.4 %
IU2	13.8	17.5	22.9	+ 9.1 %
IU3	23.4	10.4	19.8	- 3.7 %
IU4	5.0	0.9	5.7	+ 0.7 %
CU	9.1	0.4	22.9	+ 13.8 %
AL1	0.9	2.8	0	- 0.9 %
AL2	4.3	4.8	2.6	- 1.7 %
AL3	11.9	24.3	4.7	- 7.2 %
Environmental conditions				
Environment	% in the distribution range	% in the expansion range	% of the range covered by studies	Difference between % of covered and total cells
LAA	5.8	8.6	8.3	+ 2.5 %
IU	67.8	59.1	64.5	-6.3 %
CU	9.1	0.4	22.9	+ 13.8 %
AL	17.3	32.0%	7.3	- 9.99 %

Appendixes

Appendix 1 – Detailed overview of the materials and methods

1.1. Collection of studies and inclusion criteria

Data collection adopted a threefold approach. First, we extracted all those studies that were mentioned in reviews about wolf diet (Janeiro-Otero et al., 2020; Meriggi et al., 2011; Mori et al., 2017; Newsome et al., 2016; Zlatanova et al., 2014), and that were conducted in Italy between 2007 and 2023.

Moreover, we also searched for the keywords "*Canis lupus*", "*wolf*" and "*diet*" (similarly to Newsome et al., 2016) on three large datasets of scientific publications: Scopus, Web of Science, and Google Scholar. Then, from this second pool of studies, we selected those which had been carried out in Italy and were published between 2007 and 2023. As the period when data had been collected was not always reported, and results were often not split between different years, we used the year of publication to assign each study to one of the following periods: 2007-2012, 2013-2018, and 2019-2024. We also retrieved studies that were carried out after the most recent review about wolf diet (Janeiro-Otero et al., 2020), or that had been discarded by previous reviews. Finally, we also collected available grey literature about wolf diet in Italy. This included non-peer reviewed documents, such as dissertations of MSc and PhD students that had not been subsequently published in a peer-reviewed journal, or reports published by local and protected areas' authorities. As dissertations are not always adequately indexed on the archives of Italian universities, we used snowballing. First, we queried "*Dieta lupo*", the Italian translation of "*Wolf diet*" on university archives and Google. Then, we also asked other researchers and practitioners, working on wolf conservation and ecology, about further grey literature on wolf diet that we could have missed. From the pool of studies that we had obtained, we retained those for which it was possible to understand where data had been collected, with respect to the grid used by the Ministry for the Environment to quantify wolf occupancy in 2019-2021 (La Morgia et al., 2022).

1.2. Sampling frame and choice of environmental covariates

We used a 10-km resolution grid produced by the Ministry of the Environment (La Morgia et al., 2022) and by Wolf Alpine Group (2024) to identify the distribution range of wolves in peninsular Italy, until early 2024. We also downloaded distribution maps for 2007-2012 and 2013-2018 from reports of the Habitat Directive (http://reportingdirettivahabitat.isprambiente.it/) and calculated areas where wolves have expanded, during the 2019-2024 period (Fig. 1).

Then, for each cell of the grid we extracted variables related to the main food sources available to wolves. These included: anthropization and the presence of domestic livestock, wild ungulates, and the coypu (*Myocastor coypus*).

Anthropization affects wolf diet mostly through food waste, which is a nearly unlimited food source. Although wolves do not fully exploit carbohydrates (Axelsson et al., 2013), evidence from non-European countries indicate that they exploit food waste whenever available (Barocas et al., 2018; Mohammadi et al., 2019), probably by selecting for meat scraps and bones. Moreover, wolves living around human settlements could also prey on pets (Bassi et al., 2021; Kojola et al., 2022; Nowak et al., 2011). We quantified anthropization by calculating evenness of human density, quantified at a 1km resolution through the Global Human Settlement Layer (https://human-settlement.emergency.copernicus.eu/index.php), for each cell of our grid. Evenness was quantified through the Gini index, which varies from 0, when all the units of a sample have the same value of a certain measure, to 1 when one unit has the entire amount of that value. Therefore, the Gini index was positively associated with the amount of natural landscapes in each cell, with cells having the lowest values being characterized by widespread human settlements and having therefore a higher availability of food waste and domestic pets.

We also considered the abundance of domestic livestock, particularly sheep, cattle, and domestic pigs, that can be regularly preyed on by wolves (Gervasi et al., 2021). Moreover, the abundance of livestock could also account for the availability of carrion and slaughterhouse remains in the environment, important supplementary food sources for wolves (Ciucci et al., 2020; Ćirović and Penezić, 2019). For domestic livestock, we used 10 km abundance projections generated by the Food and Agriculture Organization and structured in the Gridded Livestock of the World database (GLW4, https://data.apps.fao.org/catalog/dataset/15f8c56c-5499-45d5-bd89-59ef6c026704), related to the abundance of sheep, cattle, and domestic pigs. Indeed, densities of domestic livestock had a different meaning for different livestock species. Although sheep in Italy are almost entirely raised extensively, cattle and pigs have profound differences in their husbandry type, with lowlands in Northern Italy being characterized by intensive livestock farming, which alone accounts for 30 % of the total cattle and 88% of the total pigs raised in the country (https://www.vetinfo.it/j6_statistiche/#/). Areas with a high density of cattle and pigs therefore correspond to areas with intensive livestock farming, where animals are kept in the barn and are thus not available for wolves when alive, but where wolves can feed on byproducts (e.g. placentae) and slaughtering leftovers.

For wild ungulates, we considered the five most preyed on by wolves in Italy: roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), wild boar (*Sus scrofa*), fallow deer (*Dama dama*) and Northern chamois (*Rupicapra rupicapra*) (Gazzola et al., 2007, Mattioli et al., 2011; Torretta et al., 2018). We did not consider the mouflon (*Ovis gmelini musimon*), which is distributed with scattered populations in the Italian peninsula, although occasionally it could represent an important prey (Capitani et al., 2004). Moreover, we did not consider the Sika deer (*Cervus nippon*), because its distribution in Central and Northern Italy is still uncertain (Mori et al., 2024). Neither we considered the Alpine ibex (*Capra ibex*), as it seems to play a minor role in the diet of alpine wolves (Palmegiani et al., 2013), nor did the Apennine chamois (*R. pyrenaica ornata*), due to its limited distribution and the small size of its populations (Corlatti et al., 2022). For wild ungulates, we relied on 10-km hunting yield density maps elaborated within the ENETWILD project

(ENETWILD consortium et al., 2022), using them as relative indexes for the local abundance of each wild ungulate species.

Finally, we also included the potential environmental suitability of the Italian peninsula for the coypu. Recent studies found out that the coypu can be an important prey, in some agricultural ecosystems of Central and Northern Italy (Musto et al., 2024; Ferretti et al., 2019; Marras and Marucco, 2022), probably because it is easy to prey and can attain very high densities, providing wolves with a relevant biomass (Balestrieri et al., 2016). As no abundance map was available for this species, we rather used the potential suitability of the Italian landscape, at a 1 km resolution, obtained from Schertler et al., (2020). For each cell of our grid, we calculated the median for the abundance of wild ungulates and livestock and the geometric mean for the suitability for the coypus. Although wolves in many areas of Central and Northern Europe regularly prey on other aquatic rodents, such as the Eurasian beaver (Gable et al., 2018), we did not include this species, because its population in Central and Northern Italy is still extremely small and confined to few areas (Bertolino et al., 2023).

Indeed, both ENETWILD maps and the map from Schertler et al. (2020), have their values spanning beyond the actual distribution range of the different species. Therefore, we used data from the Italian Atlas of Mammals (Loy et al., 2025), to crop these maps with respect to the effective distribution range of the different species that we considered. See Appendix 1 for a complete overview of the different variables used to identify different ecological conditions.

1.3. Data analysis and identification of areas covered by dietary studies, food resource assemblages and environments

We identified food resources assemblages as homogeneous areas within the entire Italian peninsula, based on: *i*) the Gini index of human density, *ii*) the median abundance of roe deer, red deer, wild boar, fallow deer and Northern chamois, *iii*) the median abundance of domestic pigs, sheep and cattle, i*v*) the geometric mean of the potential suitability for the coypu. To this end, we used the CLARA algorithm, an extension of Partitioning Around Medoids cluster analysis. We chose the CLARA algorithm due to the high number of cells (n = 2,510) and its robustness against non-normal data and outliers. The number of clusters was chosen by graphically exploring the silhouette width method, the elbow method, and the gap statistics method (Kassambara, 2017). Before clustering our cells, we standardized and centred our variables. Due to missing values in the raster showing the distribution of food sources, we could categorize only 89.3% of the total Italian peninsula. Almost all the cells that we did not categorize occurred in coastal areas (Fig. S4 in Appendix 2).

Then, we assigned each selected study to the various cells of the grid. Based on the information included in the analysed studies about the geographical position of their study areas, we identified the location of each study as the geographical centre of the area where biological samples had been collected. Then, we assumed that wolves for which biological samples had been collected on the centroid, could have moved in a home range of approximately 113 km^2 (Mancinelli et al., 2018; Mattioli et al., 2018) and so we generated a buffer with a radius of 6 km around each point and classified all those cells of the grid that overlapped with it. As our scope was to assess the spatial coverage of existing studies about wolf diet, and because many studies refer to the same research project, we only classified the cells of our grid as being covered by studies or not, with a dichotomous variable.

Once we identified environmental clusters, we graphically inspected how studies about wolf diet were distributed between different clusters in the 2007-2024 period, although we clusterised environmental variables in the entire Italian peninsula, we then only explored coverage in those cells that corresponded to distribution range of the wolf in early 2024 (n. cells = 2,510). We calculated both *i*) the portion of dietary studies being conducted in each different cluster and *ii*) the portion of cells of each cluster being involved in at least a dietary study. Statistical analyses were carried out in R (R Core Team 2025).

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Appendix 2 – Overview of main variables used in cluster analysis

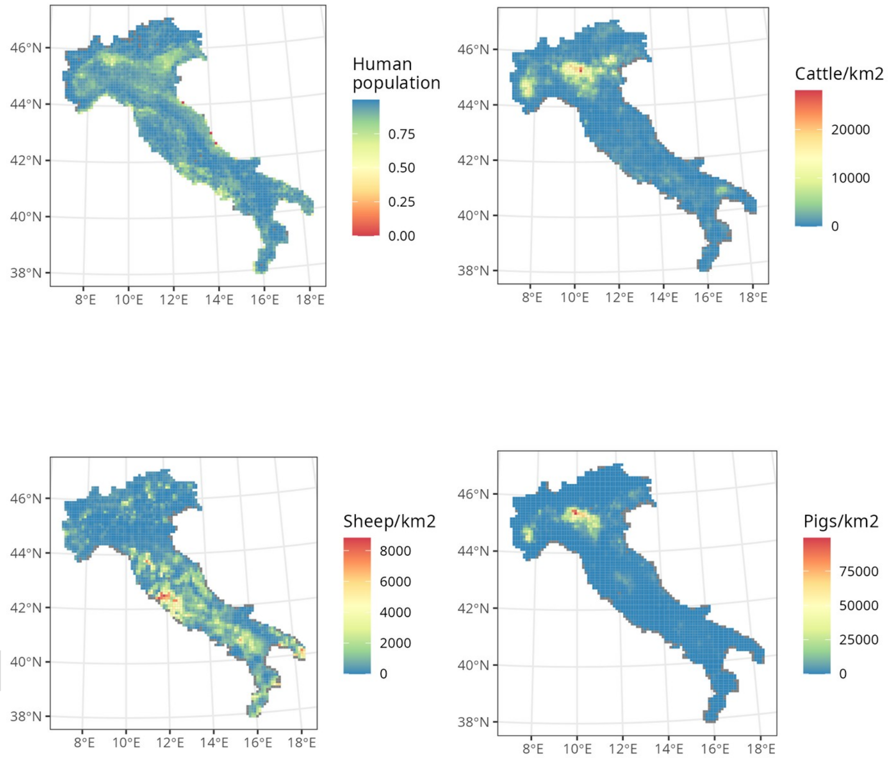

Fig. S1. Concentration of human density, expressed as the Gini index of the total number of people at a 100m scale, calculated for a cell of 10 km (lower values indicate areas with widespread anthropization) and number of domestic cattle, sheep and pigs (n. individuals/km^2).

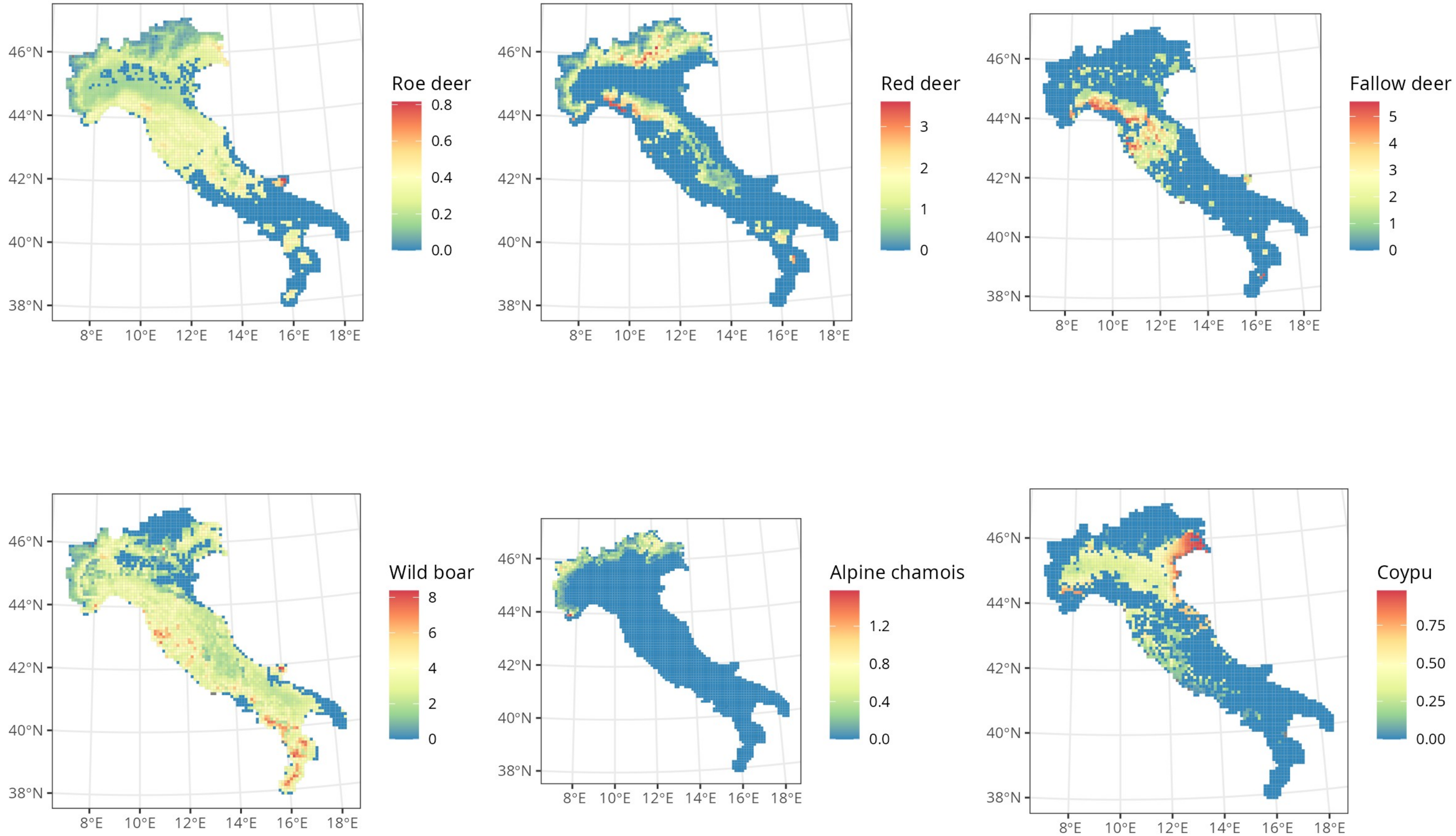

Fig. S2. Distribution of the density of the roe deer, the red deer, the fallow deer, the wild boar and the Alpine chamois (n. individuals/km ^{2}) and predicted probability of presence for the coypu.

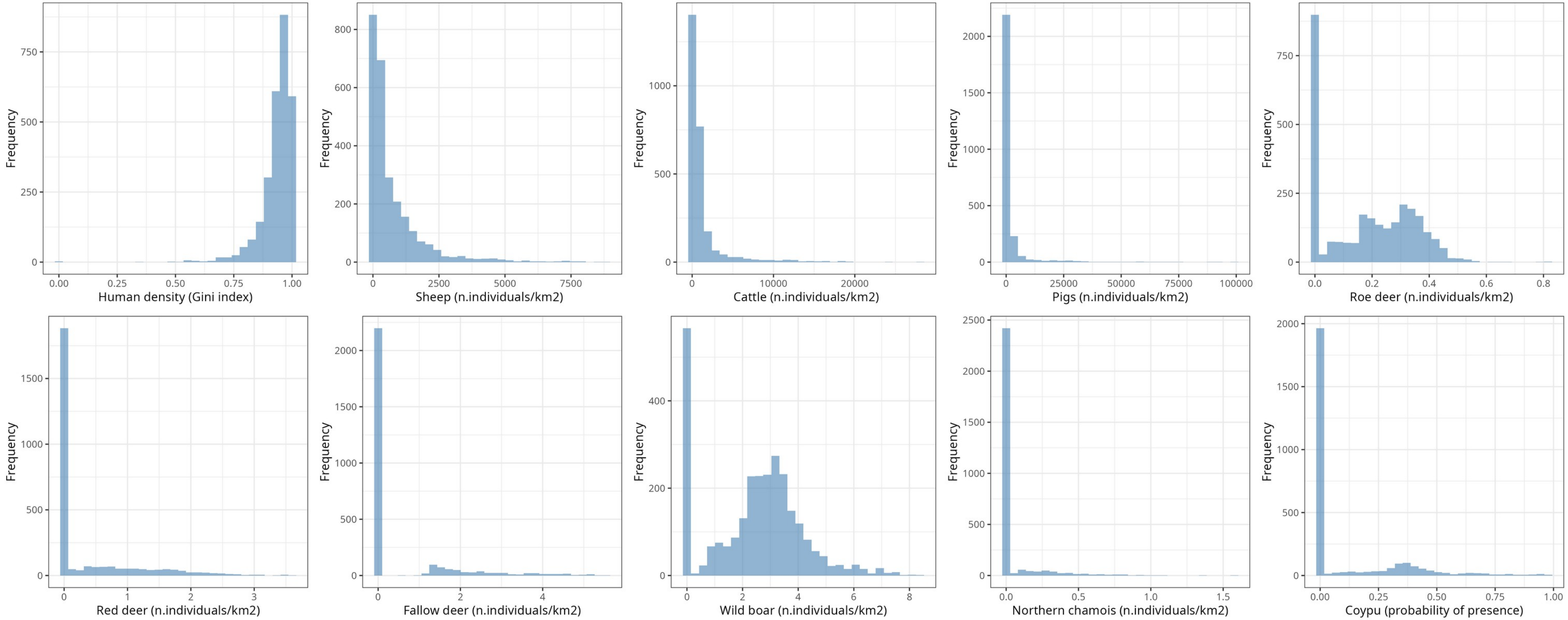

Fig. S3. Distribution of the human density, the predicted probability of presence of the coypu, as well as of the number of sheep, cattle, pigs, roe deer, red deer, fallow deer, wild boar and Northern chamois, in the cells of our grid.

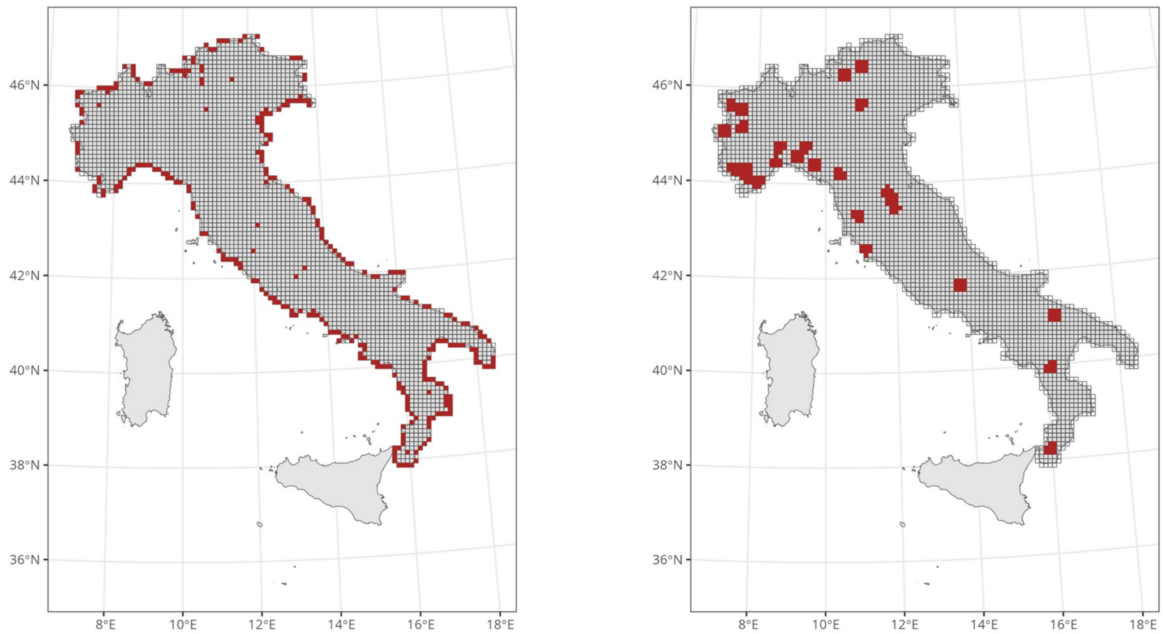

Fig. S4. Left: spatial distribution of cells that were not covered by cluster analysis, due to missing values, and which we did not assign to a particular food resource assemblage (dark). Right: spatial distribution of those cells of the grid that were covered by studies about wolf diet, between 2007 and 2024 (dark).

Appendix 3 – Final list of dietary studies included in data analysis

Source	Year	Authors	Title	Location (centroid of the study area(s))	
				Longitude	Latitude
Article	2023	Ferretti, F; Oliveira, R; Rossa, M; Belardi, I; Pacini, G; Mugnai, S; Fattorini, N; Lazzeri, L	Interactions between carnivore species: limited spatiotemporal partitioning between apex predator and smaller carnivores in a Mediterranean protected area	11.09930	42.62637
MSc thesis	2023	Macario M.	Ecologia alimentare e comportamento di marcatura del lupo (*Canis lupus*) nelle Alpi Marittime	7.69736	44.25885
Article	2023	Nardi, F; Lazzeri, L; Iannotti, N; Donini, V; Cucini, C; Belardi, I; Frati, F; Carapelli, A; Ferretti, F	Analysis of Scat for Gut Microbiome Identification in Wolves from a Mediterranean and an Alpine Area	11.09930	42.62637
Article	2023	Nardi, F; Lazzeri, L; Iannotti, N; Donini, V; Cucini, C; Belardi, I; Frati, F; Carapelli, A; Ferretti, F	Analysis of Scat for Gut Microbiome Identification in Wolves from a Mediterranean and an Alpine Area	11.06775	46.45537
Article	2023	Nardi, F; Lazzeri, L; Iannotti, N; Donini, V; Cucini, C; Belardi, I; Frati, F; Carapelli, A; Ferretti, F	Analysis of Scat for Gut Microbiome Identification in Wolves from a Mediterranean and an Alpine Area	10.58576	46.26045
Article	2021	Ferretti, F., Pacini, G., Belardi, I., Ten Cate, B., Sensi, M., Oliveira, R., ... & Lovari, S.	Recolonizing wolves and opportunistic foxes: interference or facilitation?	11.09930	42.62637
MSc thesis	2021	Rosso F.	Analisi della dieta del branco di lupi nel parco la Mandria e zone limitrofe	7.55946	45.17646
Article	2020	Bassi, E; Gazzola, A; Bongi, P; Scandura, M; Apollonio, M	Relative impact of human harvest and wolf predation on two ungulate species in Central Italy	11.92	43.66000
Article	2020	Ciucci, P; Mancinelli, S; Boitani, L; Gallo, O; Grottoli, L	Anthropogenic food subsidies hinder the ecological role of wolves: insights for conservation of apex predators in human-modified landscapes	13.79	41.80839
MSc thesis	2020	Marras F.	L'arrivo del lupo in pianura: ecologia alimentare del branco dell'Orba in provincia di Alessandria	8.61209	44.76741

Article	2019	Ferretti, F; Lovari, S; Mancino, V; Burrini, L; Rossa, M	Food habits of wolves and selection of wild ungulates in a prey-rich Mediterranean coastal area	11.09930	42.62637
MSc thesis	2018	Aleotti, S	Ecologia alimentare del lupo (*Canis lupus*) nel Parco Nazionale dell'Aspromonte	15.98859	38.22002
MSc thesis	2018	Boni C.B.	Inferring Taeniidae infection by wolf prey selection	7.74676	44.07347
Article	2018	Ciucci, P; Artoni, L; Crispino, F; Tosoni, E; Boitani, L	Inter-pack, seasonal and annual variation in prey consumed by wolves in Pollino National Park, southern Italy	16.12611	39.93111
MSc thesis	2018	Selva P.	Ecologia alimentare del lupo (*Canis lupus*) in Lessinia: un confronto fra transetti e siti di rendezvous	11.04191	45.68822
Article	2017	Bassi, E; Canu, A; Firmo, I; Mattioli, L; Scandura, M; Apollonio, M	Trophic overlap between wolves and free-ranging wolf x dog hybrids in the Apennine Mountains, Italy	11.92	43.66000
Article	2017	Bassi, E; Canu, A; Firmo, I; Mattioli, L; Scandura, M; Apollonio, M	Trophic overlap between wolves and free-ranging wolf x dog hybrids in the Apennine Mountains, Italy	11.97330	43.47138
Article	2017	Stahlberg, S; Bassi, E; Viviani, V; Apollonio, M	Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*)	11.92	43.66000
Article	2017	Stahlberg, S; Bassi, E; Viviani, V; Apollonio, M	Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*)	10.38333	44.18333
Article	2017	Stahlberg, S; Bassi, E; Viviani, V; Apollonio, M	Quantifying prey selection of Northern and Southern European wolves (*Canis lupus*)	10.95000	43.33333
Proceedings	2017	Silvestri, F., Gaudiano, L., Sorino, R., Frassanto, A.G., Corriero, G.	Analisi della dieta del lupo *Canis lupus* nel Parco Nazionale dell'Alta Murgia	16.34806	41.04806
Article	2017	Torretta, E; Serafini, M; Imbert, C; Milanesi, P; Meriggi, A	Wolves and wild ungulates in the Ligurian Alps (Western Italy): prey selection and spatial-temporal interactions	8.01461	44.05942
Article	2016	Imbert, C; Caniglia, R; Fabbri, E; Milanesi, P; Randi, E; Serafini, M; Torretta, E; Meriggi, A	Why do wolves eat livestock? Factors influencing wolf diet in northern Italy	8.01461	44.05942

Article	2016	Imbert, C; Caniglia, R; Fabbri, E; Milanesi, P; Randi, E; Serafini, M; Torretta, E; Meriggi, A	Why do wolves eat livestock? Factors influencing wolf diet in northern Italy	8.56540	44.43340
Article	2016	Imbert, C; Caniglia, R; Fabbri, E; Milanesi, P; Randi, E; Serafini, M; Torretta, E; Meriggi, A	Why do wolves eat livestock? Factors influencing wolf diet in northern Italy	9.14978	44.57441
Article	2016	Imbert, C; Caniglia, R; Fabbri, E; Milanesi, P; Randi, E; Serafini, M; Torretta, E; Meriggi, A	Why do wolves eat livestock? Factors influencing wolf diet in northern Italy	9.68675	44.36606
MSc thesis	2015	Larentis M.	L'ecologia alimentare del lupo (*Canis lupus*) in un'area di recente ricolonizzazione nel Parco Nazionale del Gran Paradiso	7.55096	45.51
Article	2015	Meriggi, A; Dagradi, V; Dondina, O; Perversi, M; Milanesi, P; Lombardini, M; Raviglione, S; Repossi, A	Short-term responses of wolf feeding habits to changes of wild and domestic ungulate abundance in Northern Italy	9.38639	44.77139
Article	2013	Palmegiani I.; Gazzola A.; Apollonio M.	Wolf diet and its impact on the ungulates community in a new recolonized area of western Alps: Gran paradiso national park	7.20944	45.59278
MSc thesis	2013	Rizzuto M.	Interazioni preda-predatore: ecologia alimentare del Lupo (*C. lupus*) e comportamento anti-predatorio del Camoscio (*R. rupicapra*) nelle Alpi Marittime	7.33708	44.30894
Article	2012	Davis, ML; Stephens, PA; Willis, SG; Bassi, E; Marcon, A; Donaggio, E; Capitani, C; Apollonio, M	Prey Selection by an Apex Predator: The Importance of Sampling Uncertainty	11.92	43.66000
Article	2012	Bassi, E; Donaggio, E; Marcon, A; Scandura, M; Apollonio, M	Trophic niche overlap and wild ungulate consumption by red fox and wolf in a mountain area in Italy	11.92	43.66000
Article	2012	Milanesi, P; Meriggi, A; Merli, E	Selection of wild ungulates by wolves *Canis lupus* (L. 1758) in an area of the Northern Apennines (North Italy)	9.38639	44.77139
Article	2011	Mattioli, L; Capitani, C; Gazzola, A; Scandura, M; Apollonio, M	Prey selection and dietary response by wolves in a high-density multi-species ungulate community	11.81984	43.79397
Article	2008	Marucco, F; Pletscher, DH; Boitani, L	Accuracy of scat sampling for carnivore diet analysis: Wolves in the Alps as a case study	7.65868	44.22310

Article	2007	Gazzola, A; Avanzinelli, E; Bertelli, I; Tolosano, A; Bertotto, P; Musso, R; Apollonio, M	The role of the wolf in shaping a multi-species ungulate community in the Italian western Alps	7.00000	45.08333

Appendix 4 – Overview of cluster analysis and the main food resource assemblages

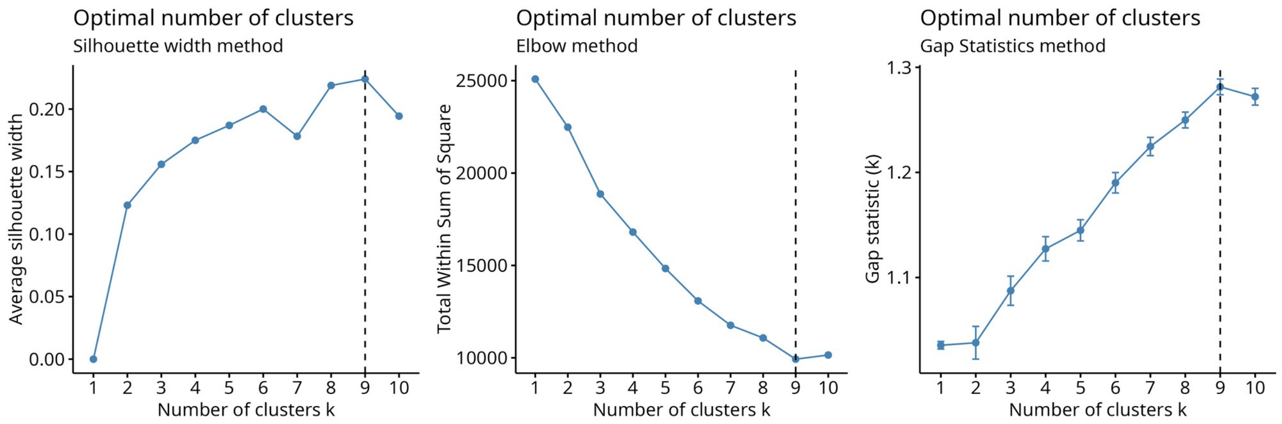

Fig. S5. Identification of the optimal number of cluster for the CLARA clustering algorithm, according to their average silhouette width, the within sum of square and the Gap statistics. For further details see Kassambara et al. (2017).

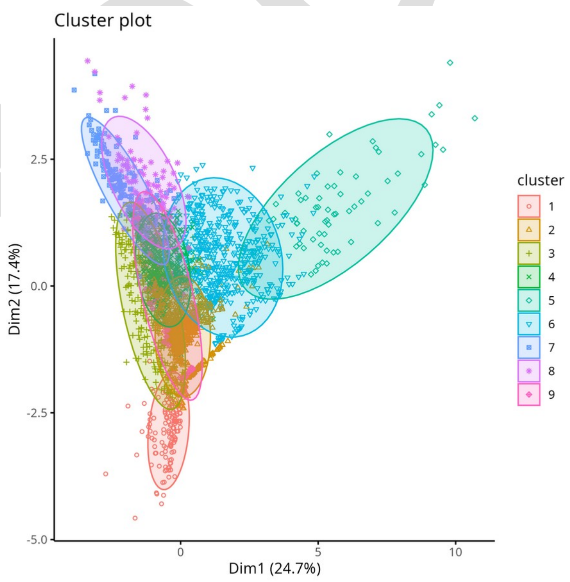

Fig. S6. Overview of clusters identified by the CLARA algorithm, with respect to the two main components of our data, obtained from PCA. See Kassambara et al. (2017).

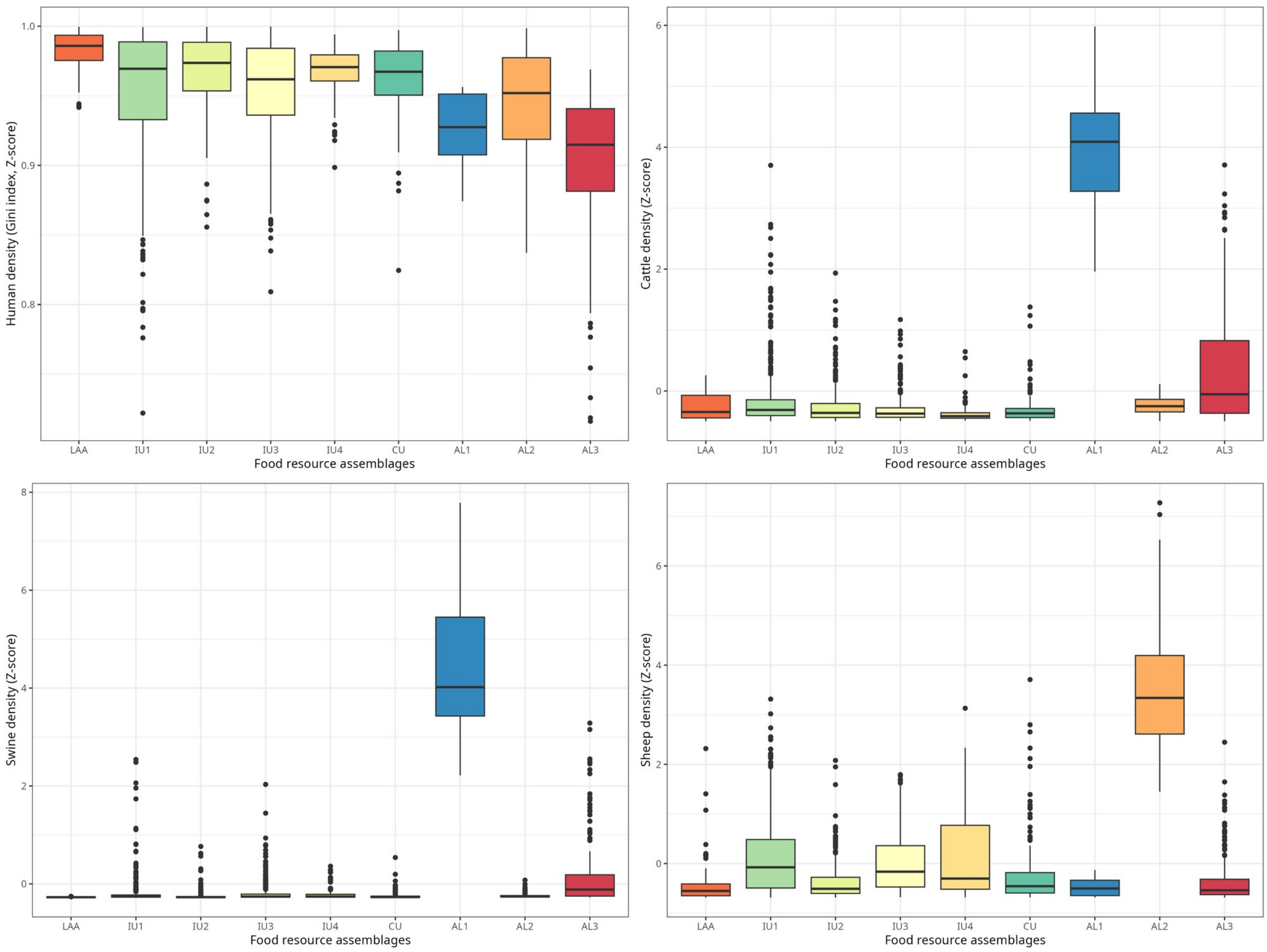

Fig. S7. Distribution of the human density, cattle density, density of sheep and density of domestic pigs, between the 9 food resource assemblages, identified through cluster analysis. Variables were converted to Z-scores, being expressed as standard deviations from the mean.

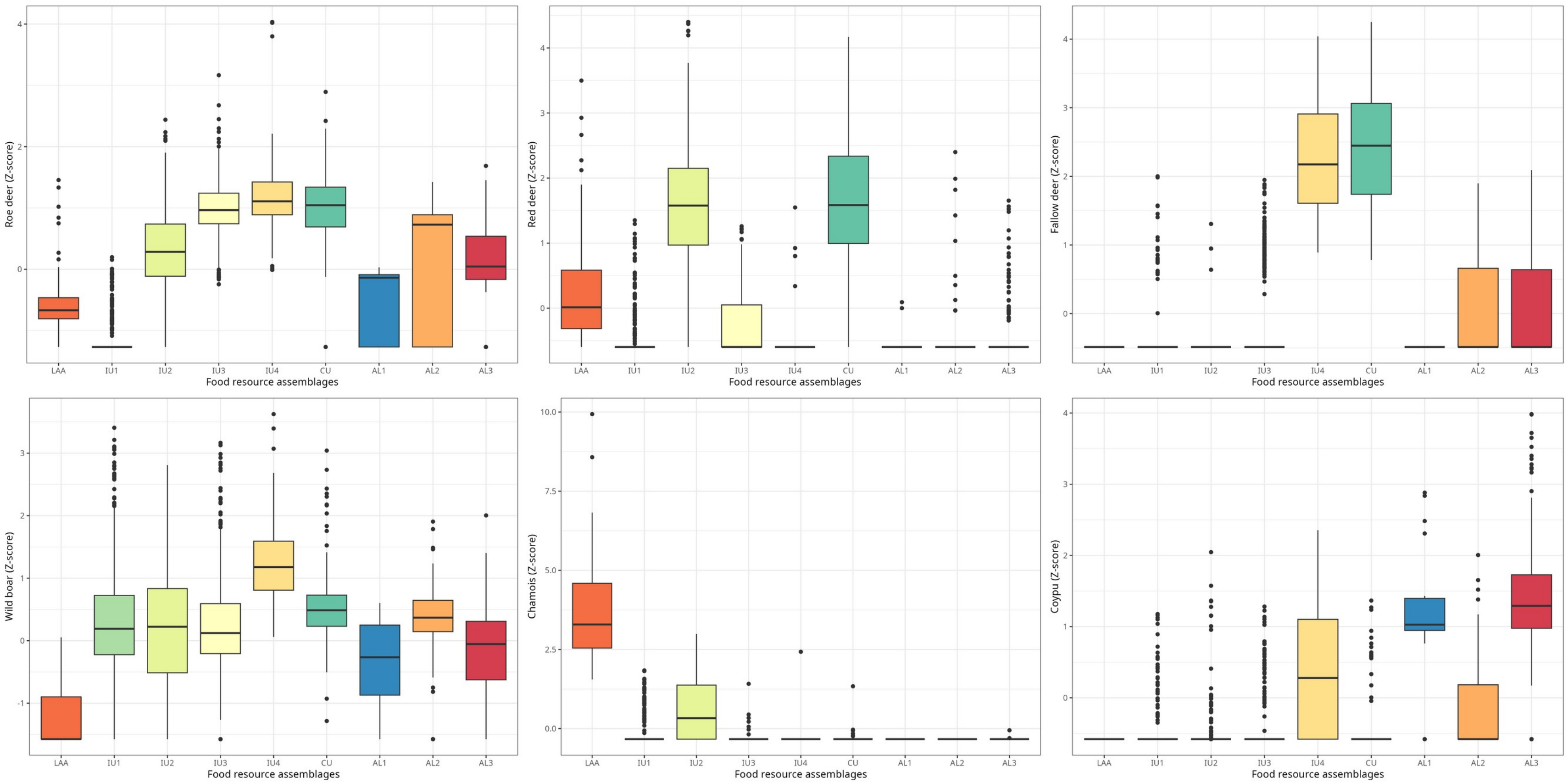

Fig. S8. Distribution of the density of roe deer, red deer, fallow deer, wild boar and Northern chamois, as well as of the predicted probability of presence for the coypu, between the 9 food resource assemblages, identified through cluster analysis. Variables were converted to Z-scores, being expressed as standard deviations from the mean.

Appendix 5 - Stomach contents of wolves that were found dead and subjected to necropsy

Fig. S9 – stomach contents of an adult female wolf who died in the province of Cremona, the presence of at least 3 small coypus (presence of 3 tails) was detected.

Fig. S10 – stomach contents of an adult female wolf who died in the province of Mantua, the presence of a limb attributable to a coypu, with hair and bones, was detected.

Fig. S11 – stomach contents of an adult male wolf who died in the province of Bologna, the presence of 4 limbs attributable to coypu can be observed.

Fig. S12 – stomach contents of an adult male wolf who died in the province of Bologna, the presence of the skin, bones and hair attributable to coypu can be observed.

Fig. S13 – stomach contents of a subadult female wolf who died in the province of Bologna, remains attributable to a rat can be observed.

Fig. S14 – stomach contents of an adult male wolf who died in the province of Pisa, remains attributable to a domestic cat can be observed.

Fig. S15 – stomach contents of a subadult male wolf who died in the province of Piacenza, remains attributable to a calf can be observed. Photo courtesy of Dr. Chiara Garbarino of the Experimental Zooprophylactic Institute of Lombardy and Emilia-Romagna.

Fig. S16 – stomach contents of an adult male wolf who died in the province of Massa Carrara, remains attributable to pig, ropes and plastic was observed.

Fig. S17 – stomach contents of a young male wolf who died in the province of Pistoia, remains attributable to pig was observed.

Fig. S18 – stomach contents of a young female wolf who died in the province of Piacenza, remains attributable to domestic poultry, small mammal and fruit was observed. Photo courtesy of Dr. Chiara Garbarino of the Experimental Zooprophylactic Institute of Lombardy and Emilia-Romagna.

Fig. S19 – stomach contents of a young female wolf who died in the province of Pisa, remains attributable to ropes and metal staples was observed.

Fig. S20 – stomach contents of an elderly female wolf who died in the province of Bologna, remains attributable to mallard and persimmons was observed.