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REVIEW

Variation in red fox *Vulpes vulpes* diet in five continents

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ABSTRACT

1. Understanding variation in the diet of widely distributed species can help us to predict how they respond to future environmental and anthropogenic changes.
2. We studied the diet of the red fox *Vulpes vulpes*, one of the world's most widely distributed carnivores. We compiled dietary data from 217 studies at 276 locations in five continents to assess how fox diet composition varied according to geographic location, climate, anthropogenic impact, and sampling method.
3. The diet of foxes showed substantial variation throughout the species' range, but with a general trend for small mammals and invertebrates to be the most frequently occurring dietary items.
4. The incidence of small and large mammals and birds in fox diets was greater away from the equator. The incidence of invertebrates and fruits increased with mean elevation, while the occurrence of medium-sized mammals and birds decreased.
5. Fox diet differed according to climatic and anthropogenic variables. Diet richness decreased with increasing temperature and precipitation. The incidence of small and large mammals decreased with increasing temperature. The incidence of birds and invertebrates decreased with increasing mean annual precipitation. Higher Human Footprint Index was associated with a lower incidence of large mammals and a higher incidence of birds and fruit in fox diet.
6. Sampling method influenced fox diet estimation: estimated percentage of small and medium-sized mammals and fruit was lower in studies based on stomach contents, while large mammals were more likely to be recorded in studies of stomach contents than in studies of scats.
7. Our study confirms the flexible and opportunistic dietary behaviour of foxes at the global scale. This behavioural trait allows them to thrive in a range of climatic conditions, and in areas with different degrees of human-induced habitat change. This knowledge can help us to place the results of local-scale fox diet studies into a broader context and to predict how foxes will respond to future environmental changes.

RESUMEN EN ESPAÑOL

1. El estudio de las variaciones de la dieta de especies ampliamente distribuidas puede ayudarnos a comprender mejor como estas especies responderán frente a cambios ambientales futuros.

2. En este estudio analizamos la dieta de uno de los mamíferos carnívoros más ampliamente distribuido, el zorro rojo *Vulpes vulpes*. Para determinar como la composición de la dieta de los zorros rojos variaba en función de la localización geográfica, el clima, los impactos antrópicos y el método de muestreo recopilamos los datos de 217 estudios llevados a cabo en 276 lugares en cinco continentes.

3. La dieta de los zorros rojos varió de forma importante a lo largo de su área de distribución, siendo los mamíferos pequeños y los invertebrados las presas más frecuentemente consumidas.

4. La frecuencia de ocurrencia de mamíferos pequeños y grandes así como de aves fue mayor en los lugares alejados del ecuador. La frecuencia de ocurrencia de los invertebrados y los frutos incrementó con el aumento de la altitud media mientras que la frecuencia de ocurrencia de mamíferos medianos y aves disminuyó.

5. La dieta de los zorros rojos estuvo influenciada por factores climáticos y antrópicos. La riqueza de la dieta disminuyó con el aumento de la temperatura y la precipitación. La frecuencia de ocurrencia de mamíferos pequeños y grandes disminuyó con el incremento de la temperatura. La frecuencia de ocurrencia de aves e invertebrados disminuyó con el aumento de la precipitación media anual. Valores elevados del índice de huella humana estuvieron asociados con una disminución de la frecuencia de ocurrencia de mamíferos grandes y un incremento de aves y frutos en la dieta de los zorros rojos.

6. La dieta de los zorros rojos también estuvo influenciada por el método de muestreo utilizado. La frecuencia de ocurrencia de mamíferos pequeños y medianos y de frutos fue inferior en estudios basados en el análisis de contenidos estomacales que en estudios basados en el análisis de excrementos. Por el contrario, la frecuencia de ocurrencia de mamíferos grandes fue mayor en los estudios basados en el análisis de contenidos estomacales que los estudios basados en el análisis de excrementos.

7. Nuestro estudio confirma el comportamiento alimentario flexible y oportunista de los zorros rojos a escala global. Estos rasgos de comportamiento permiten a los zorros rojos ocupar un amplio rango de condiciones climáticas y antrópicas. Este conocimiento puede ayudar a situar los resultados locales en un contexto global y a predecir cuales serán las respuestas de los zorros rojos frente a cambios ambientales futuros.

INTRODUCTION

A key defining feature of a species' niche and ecological roles is its diet (Pocheville 2015). What an animal species eats influences its trophic position, how it moves around, and which other species it interacts with, among many other behaviours. While diets are flexible, predators have evolved to forage optimally on certain prey types or species (Hayward et al. 2011, 2016). The mechanisms that determine optimal foraging behaviour include adaptive responses to prey availability, food quality, energy required to handle prey (Pyke et al. 1977, Sundell et al. 2003), and predation risk from larger co-occurring predators (Haswell et al. 2018).

Ecological and climatic conditions determine animal distributions and, in turn, diet composition, so the study of intraspecific diet variation using large biogeographical datasets provides a powerful means to understand the ecology of Carnivora. For instance, regional- and continental-scale studies of dietary variation have been conducted for feral cats *Felis catus* (Doherty et al. 2015),

wildcats *Felis silvestris* (Lozano et al. 2006), badgers *Meles meles* (Goszczyński et al. 2000), polecats *Mustela putorius* (Lodé 1997), common genets *Genetta genetta* (Virgós et al. 1999), otters *Lutra lutra* (Clavero et al. 2003), martens *Martes* spp. (Zhou et al. 2011), and dingoes *Canis dingo* (Doherty et al. 2019). Knowledge about spatial differences in feeding behaviour can contribute to understanding the foraging strategies used by generalist predators to exploit a wide range of food resources optimally.

Among generalist medium-sized carnivores, the red fox *Vulpes vulpes* (hereafter 'fox') is a prime example of a species with adaptive foraging behaviour that allows it to exploit alternative prey when the abundance of its main prey decreases (Kjellander & Nordström 2003). In addition, foxes are able to survive in a range of environments, including highly modified urban and agricultural areas where they exploit anthropogenic foods (Harris 1981, Saunders et al. 1993, Contesse et al. 2004, Bateman & Fleming 2012) and domestic poultry and pets (Lewis et al. 1993). As prey availability varies with habitat and environmental factors, it is not surprising that fox diet composition varies with geographic location. A regional-scale review of red fox diet in the Iberian Peninsula found that invertebrates were the most frequently reported food of foxes followed by fruit/seeds, small mammals, lagomorphs, carrion/garbage, birds, and reptiles (Díaz-Ruiz et al. 2013). Throughout Europe, rodents are the principal food of foxes, followed by plants, invertebrates, birds, lagomorphs, reptiles, and amphibians (Soe et al. 2017). In Australia, where the fox has been introduced, its diet mainly comprises small and medium-sized mammals, livestock, reptiles, birds, invertebrates, and vegetation (Fleming et al. 2021). Notwithstanding these regional- and continental-scale studies of fox diet, quantitative studies describing worldwide biogeographical patterns in fox diet composition have not been undertaken. Understanding of geographic variation in red fox diet at a global scale can be used to predict how this widespread species will respond and adapt to future land use and climate change.

We compiled the most complete dataset to date to assess variation in fox diet composition throughout its global geographic range. First, we assessed geographic patterns in the dietary ecology of foxes, particularly among continents. Second, we analysed changes in consumption of different foods and diet richness in relation to geographic variables (absolute latitude, mean elevation), climatic variables (mean annual temperature, mean annual precipitation), and an anthropogenic variable (Human Footprint Index, HFI). We used the results to test the following key predictions relating to environmental and anthropogenic factors (Table 1):

1. Environmentally extreme conditions for life increase in their incidence with increasing absolute latitude, reducing species richness in higher latitudes (Kent 2005). In line with regional-scale and continental-scale studies of fox diet (Díaz-Ruiz et al. 2013, Soe et al. 2017), we predict fewer medium-sized mammals and invertebrates in the diet with increasing absolute latitude, and therefore a relatively greater occurrence of small mammals, birds, and fruit in the diet. We predict lower diet richness with increasing absolute latitude at a continental and global scale, as has been shown for Europe (Soe et al. 2017; but not at the regional scale, Díaz-Ruiz et al. 2013).

2. The elevation gradient shares climatic features with latitudinal gradients, including decreasing species richness (Rahbek 1995) and abundance (Lomolino 2001) as elevation increases. Accordingly, and as found by Díaz-Ruiz et al. (2013), we predict a greater occurrence of small mammals but fewer medium-sized mammals in fox diet as elevation increases. We also predict lower diet richness with increasing elevation.

3. Temperature influences the activity of ectothermic prey species and is therefore likely to influence the composition of carnivore diets. For warmer locations, we therefore predict a greater occurrence of invertebrates in fox diet and higher diet richness (Díaz-Ruiz et al. 2013, Soe et al. 2017, Fleming et al. 2021).

4. Rainfall is correlated with environmental productivity, and we therefore predict more fruit in the diet of foxes from higher rainfall locations and greater diet richness with increasing precipitation.

5. We predict that locations with a greater HFI will have a greater occurrence of novel anthropogenic food resources (garbage; Contesse et al. 2004, Bateman & Fleming 2012, Dawson et al. 2016), which is likely to decrease fox dietary richness (Soe et al. 2017).

6. The type of sample (i.e. stomachs or scats) can influence prey detection due to differential digestibility and ease of prey identification (Fleming et al. 2021). Because of the direct relationship between prey mass and digestibility (Ferreras & Fernandez-de-Simon 2019), we predict a higher occurrence of large mammals and lower occurrence of small and medium-sized mammals and birds in studies that analysed stomach contents rather than scats.

METHODS

Literature search and dataset construction

We carried out a quantitative literature review to select studies focused on fox diet, published before or during 2018. We used ("*Vulpes vulpes*" OR fox) AND (diet OR predation OR ecology) as keywords in ISI Web of Science,

Table 1. Key predictions tested herein on the global dietary patterns of red foxes *Vulpes vulpes*

Predictor variable	Predicted direction of relationship(s)	Supporting reference(s)	Results of this study (based on latitude models)
↑ Absolute latitude	↑ Small mammals, birds, fruit ↓ Medium-sized mammals, invertebrates ↓ Diet richness	Díaz-Ruiz et al. (2013), Soe et al. (2017)	↑ Small and large mammals, birds
↑ Elevation	↑ Small mammals ↓ Medium-sized mammals ↓ Diet richness	Díaz-Ruiz et al. (2013)	↑ Invertebrates, fruit ↓ Medium-sized mammals
↑ Temperature	↑ Invertebrates ↑ Diet richness	Díaz-Ruiz et al. (2013), Soe et al. (2017), Fleming et al. (2021)	
↑ Precipitation	↑ Fruit ↑ Diet richness	Díaz-Ruiz et al. (2013)	↓ Birds, invertebrates ↓ Diet richness
↑ Human Footprint Index (HFI)	↓ Diet richness	Bateman and Fleming (2012), Dawson et al. (2016), Soe et al. (2017)	↓ Large mammals ↑ Birds, fruit
↑ Type of sample (stomach–scat ratio; all scats = 0, all stomachs = 1)	↑ Large mammals ↓ Small and medium-sized mammals, birds	Ferreras and Fernandez-de-Simon (2019), Fleming et al. (2021)	↑ Large mammals ↓ Small and medium-sized mammals, fruit

JSTOR, and Google Scholar. For each study, we downloaded the title, abstract, authors, year, and journal name. Additionally, we examined the reference lists of all articles that were identified in our initial dataset to ensure key literature was not missed.

We selected studies reporting frequency of occurrence (FO, i.e. the number of individual samples where a food item was present as a percentage of the total number of samples) of food items consumed by foxes, from scats, stomachs, or both scats and stomachs (Appendices S1 and S2). FO was selected for comparison of studies as other metrics have not been used as consistently or as widely. To ensure comparability in dietary metrics, we excluded 40 studies that only reported diet composition in relation to total diet contents, e.g. percentage or relative weight/volume, relative FO, percentage volume, prey found around dens, or percentage of hair sampled. We included studies with ≥16 samples that collected fox diet data either in a single year or over many years, as well as either in a single location or in a small geographical region (e.g. county or district). To limit pseudoreplication, when several locations, years, or seasons were sampled in the same study, we pooled FO of each food category across sites <80 km apart, or for the same sites sampled across several years or seasons. We chose this site distance based on fox home range size (median = 3.25 km^2; Main et al. 2019), distances travelled by foxes (11 km, Coman et al. 1991; up to 8 km, Tsukada 1997), and maximum dispersal distance (>80 km; Trewhella et al. 1988, Newsome et al. 2017), to reduce the probability that a fox could frequently travel between study sites. This resulted in a total of 217 fox diet studies included in our analyses (Fig. 1).

Diet data

We used a consistent set of 13 food categories to report on fox diet: 1) small mammals (adult weight <500 g), 2) medium-sized mammals (500–6999 g), 3) large mammals (≥7000 g), 4) unidentified mammals, 5) birds, 6) invertebrates, 7) reptiles, 8) amphibians, 9) fish, 10) fruit, 11) vegetation, 12) garbage (i.e. human-related materials and discarded food), and 13) unidentified food. These food categories were chosen because they have been widely reported as foods consumed by foxes in many parts of the world (Abe 1975, Catling 1988, Jankowiak et al. 2008, Drygala et al. 2014). If the authors of a study pooled data for multiple mammal sizes in only one food category, we classed this category as 'unidentified mammals'. In those instances, we recorded 'not applicable' against the individual mammal size categories. Also, if a primary source reported on food types that encompassed more than one of our categories (e.g. 'fruit and vegetation' or 'amphibians and reptiles'), we considered them as 'unidentified food'. Values reported as <1% and <0.01% were included in our dataset as 0.5% and 0.005%, respectively. If a value or comment was not provided for a food category in the study, we coded it as 'not applicable' in our dataset. When the food category was mentioned in the text or accounted for but not recorded in the diet, we included a zero value in our dataset. Where food categories used in primary sources differed from the set of categories we adopted, we used combinatorial probabilities (for more details, see Murphy et al 2019) to pool FO of food categories (i.e. number of individuals of each food or food occurrences over sample size).

Spatial variables

We created a 20 km circular buffer around each study location to estimate mean annual temperature and precipitation, elevation, and HFI. Mean annual temperature, precipitation, and elevation at 5 m resolution were sourced from the WorldClim dataset (www.wordclim.org). We quantified anthropogenic influence using the HFI layer version 2, 1995–2004 (Wildlife Conservation Society – WCS 2005); this database represents a global spatial dataset of the HFI normalised by biome and realm. Global HFI is estimated using population density, human land use, infrastructure (e.g. built-up areas, night-time lights), and human access (e.g. coastlines, roads, railroads). Given the range in publication dates among papers included in our study (1935–2018), we fitted for each food category one model using the full dataset ($n = 217$ fox diet studies) and another only including papers carried out between 1995 and 2004 ($n = 59$ fox diet studies) to match the temporal resolution of the HFI layer (Appendix S3). We found similar patterns between those models; thus, we used the full dataset for subsequent analyses (Appendix S4).

Predictor variables were not highly correlated with each other ($r \leq 0.62$). To confirm that our choice of a 20 km buffer was appropriate, we tested the degree of correlation between three different buffer radius values (i.e. 5, 10, and 20 km) and found that correlation coefficients were very high (temperature: $r > 0.99$; precipitation: $r > 0.99$; elevation: $r > 0.96$; and HFI: $r > 0.90$). This indicates that our inferences are unlikely to be influenced greatly by our choice of buffer distance.

Analysis of global and continental fox diet

We assessed patterns of fox diet composition (excluding unidentified birds, unidentified mammals, and unidentified food) among and within continents using the analysis of similarity (ANOSIM) in the 'vegan' package (version 2.5-7; Oksanen et al. 2020) in R (version 4.1.2; R Core Team 2021). We excluded Africa from these analyses because only two studies from Africa met our criteria. ANOSIM provided a measure of dissimilarity (R) among and within continents. Dissimilarity (R) values range between −1 (i.e. low dissimilarity) and +1 (i.e. high dissimilarity between groups). Because ANOSIM requires a complete dataset, we considered food category absences as genuine absences. We used Euclidean distances to ordinate fox diet composition in two dimensions using 300 random starts. We performed Monte Carlo randomisation to determine the significance of the final stress values and used ANOSIM to test the hypothesis of no difference between two or more groups, against 999 random permutations of the data, followed by pairwise ANOSIMs.

Analysis of biogeographical patterns of fox diet

We modelled the relationship between fox dietary variables as dependent variables (i.e. FO of each food category, as well as total diet richness, diversity, and equitability) in separate analyses using the predictor variables of absolute latitude, mean elevation, mean annual temperature, mean annual precipitation, HFI, and sampling method (stomach to scat ratio: all scats = 0 and all stomachs = 1). We tested for multicollinearity among our predictor variables using variance inflation factors calculated in the 'car' package (version 3.0.11; Fox & Weisberg 2019). There was high collinearity between absolute latitude and temperature (variance inflation factor >5); thus, we did not include those two variables in the same models. We fitted generalised linear models with predictors of either temperature or absolute latitude, plus precipitation, elevation, and the HFI. That is, we fitted two models for each response variable. We used the 'lme4' package (version 1.1.27.1; Bates et al. 2015) in R to fit generalised linear models. All predictor variables were mean-standardised before they were added to the model. We assessed model fit using the quartile–quartile plot function provided in the 'DHARMa' package (Hartig 2021). This analysis indicated overdispersion of residuals in all food categories; thus, a Tweedie generalised linear model was fitted. The alpha value was set in each model to maximise the normality of the residuals as indicated using the 'Tweedie' package in R (Dunn & Smyth 2005, 2008, Dunn 2017). For each food category, models of all combinations of variables were assessed using *dredge* in the 'MuMIn' package in R (Barton 2020), which were then weighted according to the Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson 2002) or Tweedie-AIC value (t-AIC; Dunn 2017). We averaged estimates across models that were within two units of the best model and selected predictor variables included in those models to carry out model predictions. We present means and 95% confidence intervals for significant covariates ($P < 0.05$).

RESULTS

Global and continental fox diet

At the global scale, the most commonly reported food categories in fox diets were small mammals (mean FO: $45 \pm 4\%$) and invertebrates (FO: $41 \pm 4\%$; Fig. 2, Appendix S5). The composition of fox diet differed significantly among continents ($R = 0.090$; $P = 0.001$), and there were different degrees of dietary overlap in pairwise comparisons (Table 2). Key differences between continents (excluding Africa) included a lower occurrence of small
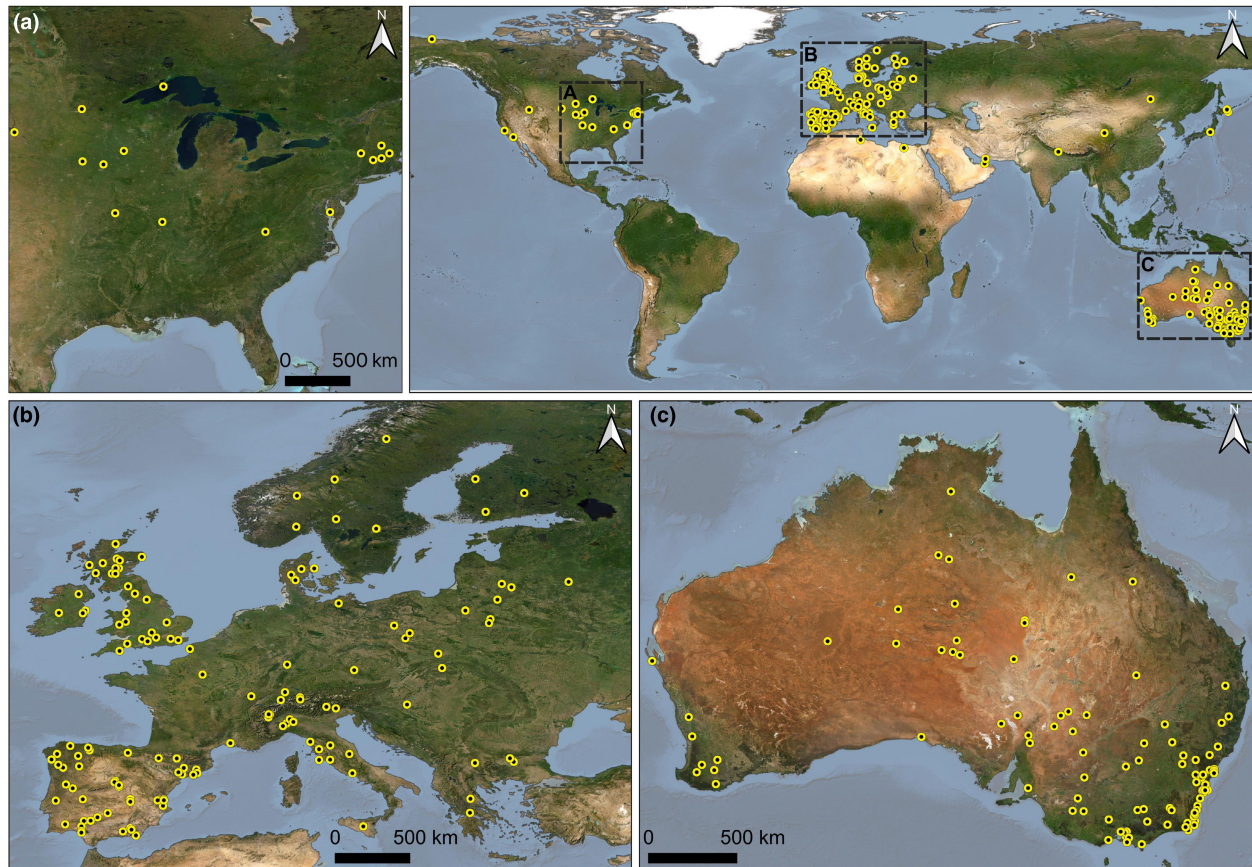
Fig. 1. Geographical distribution of the 217 red fox *Vulpes vulpes* diet studies (points) included in this review, globally (top right; 217 studies), and in more detail in the eastern USA (a), Europe (b), and Australia (c).

mammals in Australia (mean FO: $23 \pm 4\%$), lower occurrence of medium-sized mammals in Asia (mean FO: $4 \pm 7\%$), higher occurrence of birds (Europe: mean FO: $36 \pm 5\%$; North America: mean FO: $40 \pm 15\%$), fruit (Europe: mean FO: $37 \pm 6\%$; North America: mean FO: $39 \pm 18\%$), and garbage (Europe: mean FO: $18 \pm 5\%$; North America: mean FO: $8 \pm 10\%$) in Europe and North America, as well as a higher occurrence of reptiles in Australia (mean FO: $10 \pm 3\%$; Fig. 2, Appendix S3). Three pairwise comparisons between continents were significant, with Australia and Europe having the highest similarity ($R = 0.092$; $P = 0.001$; Appendix S6) and Australia and North America the lowest ($R = 0.386$; $P = 0.001$; Table 2, Appendix S6).

Biogeographical patterns of fox diet

In the latitude model, fox diet richness decreased with increasing precipitation ($t = -2.174$, $P = 0.031$; Fig. 3, Appendix S7). In the temperature model, fox diet richness decreased with both increasing temperature ($t = -3.302$, $P = 0.001$) and precipitation ($t = -3.450$, $P < 0.001$; Appendices S8 and S9).

In latitude models, the FO of small mammals ($t = 8.662$, $P < 0.001$), large mammals ($t = 3.720$, $P < 0.001$), and birds ($t = 7.302$, $P < 0.001$) in fox diet increased with increasing absolute latitude (Fig. 4a–c, Appendix S7). The FO of invertebrates ($t = 2.545$, $P = 0.011$) and fruit ($t = 3.308$, $P = 0.001$) increased with increasing elevation (Fig. 4e,f), while the FO of medium-sized mammals decreased ($t = -2.300$, $P = 0.022$; Fig. 4d). In the temperature model, the FO of birds decreased with increasing elevation ($t = -3.059$, $P = 0.002$; Appendices S8 and S10).

In the latitude model, bird ($t = -2.920$, $P = 0.004$) and invertebrate ($t = -3.113$, $P = 0.002$) FO decreased with increasing precipitation (Fig. 4g,h, Appendix S7). There was a lower incidence of large mammals ($t = -2.805$, $P = 0.005$) with increasing HFI (Fig. 4i), while bird ($t = 2.259$, $P = 0.025$) and fruit ($t = 4.727$, $P < 0.001$) FO in fox diet increased (Fig. 4j,k, Appendix S7). These results were similar in temperature models (Appendices S8 and S10). The FO of small mammals ($t = -8.067$, $P < 0.001$), large mammals ($t = -2.531$, $P = 0.012$), and birds ($t = -6.090$, $P < 0.001$) decreased with increased temperature (Appendices S8 and S10).

Influence of sample type on fox diet

In latitude models, the FO of some food categories in fox diet was influenced by the sampling method. Small mammals ($t = -2.824$, $P = 0.005$), medium-sized mammals ($t = -2.219$, $P = 0.027$), and fruit ($t = -2.867$, $P = 0.005$) were more likely to be recorded in studies that analysed scats rather than stomach contents (Fig. 4l,m,o; Appendix S7). By contrast, large mammals ($t = 2.326$, $P = 0.021$) were more likely to be recorded in studies that analysed stomach contents rather than scats (Fig. 4n, Appendix S7). Similar results were found for temperature models (Appendices S8 and S10).

DISCUSSION

Based on the collation of a large dataset of comparable dietary studies from most of the global range of the fox, we assessed geographic variation in fox diet and tested predictions in relation to environmental and anthropogenic drivers. We found that fox diet composition varied among continents and that geographic, climatic, and anthropogenic variables influenced fox diet richness. These results are likely to reflect differences in both prey availability and anthropogenic influences. Moreover, the sample type used in studies (stomach-to-scat ratio) influenced the occurrence of mammals and fruit in fox diet samples.

Global and continental fox diet

Globally, fox diets were dominated by the occurrence of small mammals and invertebrates, and we found similarities in fox diet composition among some continents (e.g. Australia and Europe). Our results for global fox diet composition accord with previous studies at smaller continental or regional scales, showing that small mammals and invertebrates are principal food items in terms of FO, including in Europe (Soe et al. 2017), the Iberian Peninsula (Díaz-Ruiz et al. 2013), and Australia (Fleming et al. 2021). Consumption of these food categories may be related to their relative availability, as has been demonstrated at local scales (Pavey et al. 2008, Cupples et al. 2011, Spencer et al. 2014), and to prey preferences exhibited by predators (Randa et al. 2009, Spencer et al. 2017). Less abundant prey may be preferred by foxes over more abundant prey if less abundant prey species are naïve to fox predation, making them easier to capture (Graham et al. 2017), or if foxes have evolved adaptations to prey more successfully on those species (optimal foraging). This is especially true within the introduced range of foxes, where foxes can represent a direct (Salo et al. 2007) and indirect (Molsher et al. 2017) threat to naïve prey (Woinarski et al. 2015, Radford et al. 2018).

Latitudinal gradients

One of the most widely recognised phenomena in ecology is the decline in species diversity with increasing absolute latitude (Hillebrand 2004). Many climatic and other ecological variables, which also vary with absolute latitude, are likely to drive these species distribution patterns, and therefore the prey available to carnivores such as the fox. Fox diet richness, however, did not change with absolute latitude. This result accords with Díaz-Ruiz et al. (2013) who found no relationship between fox diet richness and latitude in the Iberian Peninsula. In contrast, throughout Europe, fox diet diversity has been shown to decrease with latitude in cold but not in warm periods (Soe et al. 2017). Relationships between diet composition and latitude have also been found for other medium-sized carnivores such as American martens *Martes americana* in the Holarctic region (Zhou et al. 2011).

In support of our predictions, small mammal and bird FO in fox diet increased with increasing absolute latitude, which may be due to cooler temperatures away from the equator. Indeed, the biological and ecological processes of endotherms such as small mammals and birds are somewhat independent of ambient temperature, while those of ectotherms (i.e. amphibians, reptiles, and invertebrates) are directly linked with ambient temperature (e.g. Caldwell et al. 2017, Brandt et al. 2018, Jara et al. 2019). Also, the diversity and possibly abundance of reptiles decrease away from the equator (Roll et al. 2017). Thus, it may be that endothermic prey (birds and mammals) are more likely to be consumed by foxes than ectothermic prey (e.g. reptiles) at higher latitudes. Similar latitudinal patterns have been found throughout Europe, where mammals (mainly rodents) and birds were more common in fox diet with increasing latitude (Soe et al. 2017). Also, at the regional scale in the Iberian Peninsula, small mammal FO in fox diet was higher at northern than at southern latitudes (Díaz-Ruiz et al. 2013). We also found that large mammal FO in fox diet increased with increasing absolute latitude. The weight of prey in this food category ($\geq$7000 g) suggests that it is mostly consumed by foxes as carrion. However, the fox use of prey in this food category could also be related in part to the higher densities (>250 head km^{-2}) of large domestic mammals (livestock) away from the equator (Robinson et al. 2014).

Elevational gradients

Like latitude, elevation also has strong effects on ecological community composition and climatic variables (Heaney 2001, McCain 2009), which may in turn influence
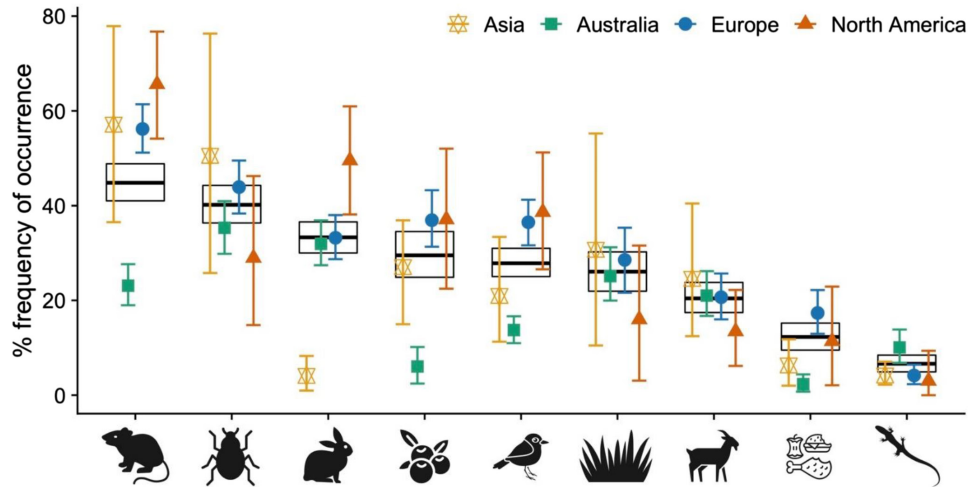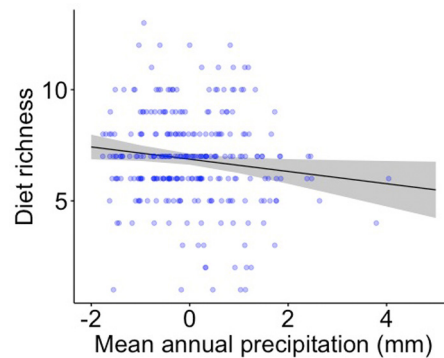
Fig. 2. Occurrence of key food categories in the diet of red foxes *Vulpes vulpes*. Food categories, from left to right, are as follows: small mammals, invertebrates, medium-sized mammals, fruit, birds, vegetation, large mammals, garbage, and reptiles. The symbols represent continental means ±95% confidence intervals. The black boxes represent global means ±95% confidence intervals. A continental mean is not shown for Africa because only two studies were available, but those two studies are included in the global means. Infrequently taken and unidentified food categories are not shown here (i.e. unidentified mammals, amphibians, fish, unidentified food), but means and standard deviations of all food categories are presented in Appendix S5.

Table 2. Analysis of similarity (ANOSIM) results of fox *Vulpes vulpes* dietary composition among continents. Values are the ANOSIM *R* statistic for the difference between each pair of continents, with the respective *P* value in parentheses; bold values are significant at $P < 0.05$. Dissimilarity (*R*) values range between −1 (i.e. low dissimilarity) and +1 (i.e. high dissimilarity between groups). Fox diet is similar in Asia, Europe, and North America but different in Australia

	Asia	Australia	Europe
Asia	–	–	–
Australia	0.320 (**0.003**)	–	–
Europe	−0.056 (0.659)	0.092 (**0.001**)	–
North America	0.142 (0.100)	0.386 (**0.001**)	−0.036 (0.662)

Fig. 3. Relationship between mean annual precipitation (mm) and red fox diet richness estimated by generalised linear models. Dots represent observed values, solid lines represent estimates, and shading denotes 95% confidence intervals of the modelled mean relationship. Predictor variables were mean-standardised.

what carnivores eat. For instance, the diet of Eurasian otters *Lutra lutra* is characterised by a greater proportion of some food categories (e.g. amphibians) at higher elevations (Remonti et al. 2009). At a regional level on the Iberian Peninsula, medium-sized mammal FO in fox diet decreased with increasing elevation (Díaz-Ruiz et al. 2013). We found the same results at the global scale, and also found that invertebrate and fruit FO in fox diet increased with increasing elevation. The altitudinal trend of consumption of invertebrates and fruit by foxes has also been described at a local scale in the Sumava Mountains in the Czech Republic (Hartová-Nentvichová et al. 2010). The decrease in bird FO in fox diet with increasing elevation that we demonstrated is likely to reflect the decrease in bird species richness with increasing elevation (McCain 2009).

Climatic effects

Our results highlight the importance of considering the effects of both temperature and precipitation on carnivore diets across large spatial scales. The composition of carnivore diets has been assessed in different seasons (Díaz-Ruiz et al. 2013), cold and warm periods (Soe et al. 2017), Mediterranean and non-Mediterranean climates (Lozano et al. 2006), and across different bioclimatic regions (Doherty et al. 2015, 2019, Fleming et al. 2021). Temperature and precipitation can have

LATITUDE

ELEVATION

PRECIPITATION

HFI

TYPE OF SAMPLE
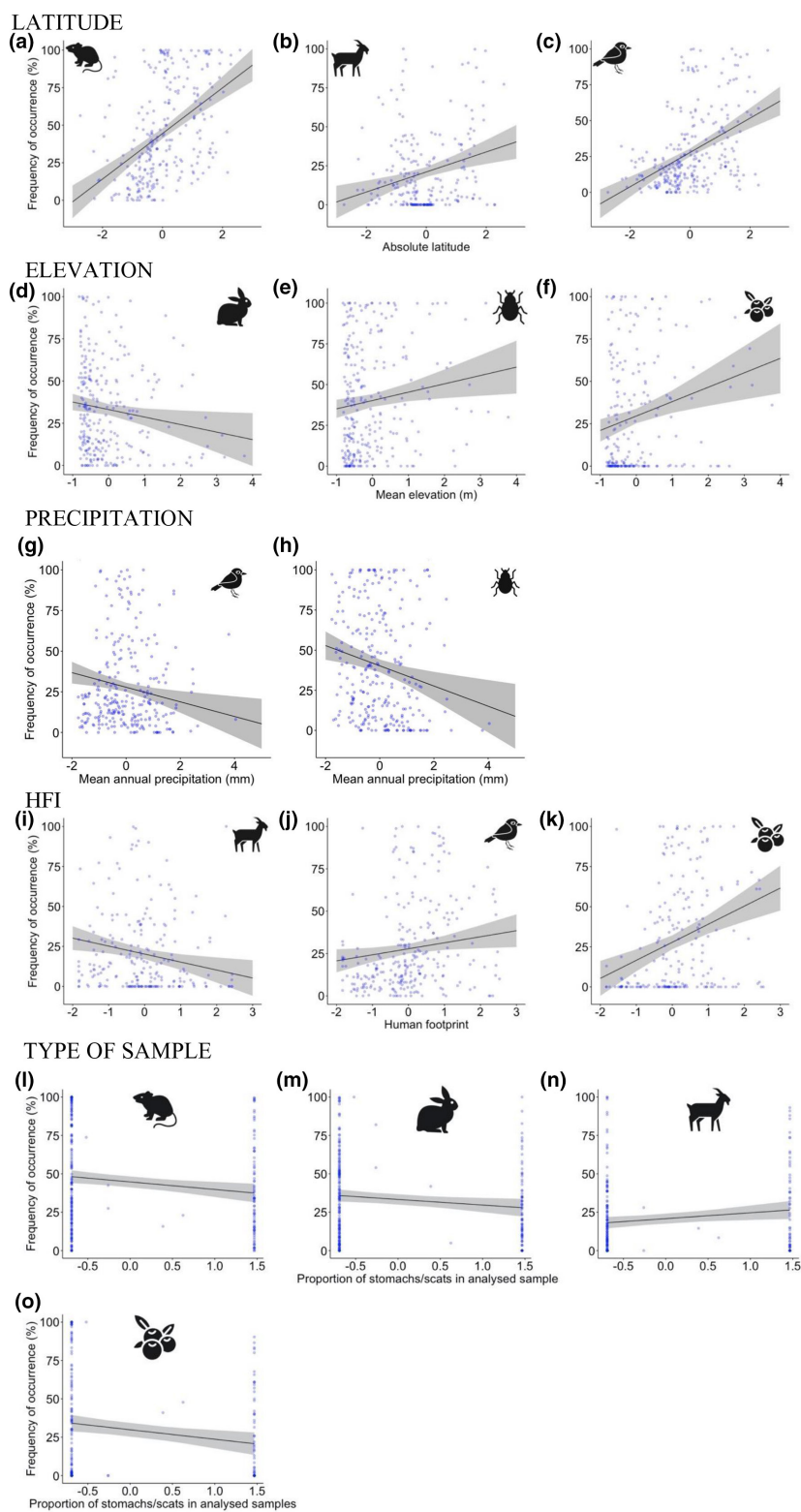
Fig. 4. Relationships between absolute latitude (m; a–c), mean elevation (m; d–f), mean annual precipitation (mm; g, h), Human Footprint Index (HFI; i–k), and sample type (stomach–scat ratio; l–o) and frequency of occurrence of food categories (see Fig. 2 for category names) in the diet of red foxes *Vulpes vulpes*, estimated by generalised linear models. Dots represent observed values, solid lines represent estimates, and shading denotes 95% confidence intervals of the modelled mean relationship. Predictor variables were mean-standardised.

different effects (sometimes even counteracting each other) depending on the ecology of predators and prey. We found that fox diet richness decreased with both temperature and precipitation, and the occurrence of many food categories in fox diets varied with precipitation but not with temperature.

The finding that diet richness decreased as both temperature and precipitation increased was contrary to our predictions. This result suggests that, under climate change scenarios, fox diet composition could shift with changing prey availability, particularly given the behavioural adaptability of this species. Diet shifts due to climate change have been demonstrated for other carnivores such as the Endangered eastern quoll *Dasyurus viverrinus* in Australia (Fancourt et al. 2018) and the polar bear *Ursus maritimus* in Canada (Gormezano & Rockwell 2013). Broader knowledge of the influence of climate variables (e.g. temperature and precipitation) on the relative abundance of prey types and hence carnivore diet composition will enhance our understanding of climate change effects on predator–prey interactions.

The activity of some prey is influenced by temperature, which may in turn influence their vulnerability to predation. Consequently, the thermoregulatory strategy of prey can be an important determinant of spatial and temporal variation in carnivore diets. For example, throughout Europe, reptiles (and amphibians) and invertebrates are consumed more by foxes in the warm period than in the cold period (Soe et al. 2017), and in Australia, there is an increasing occurrence of reptiles and frogs in fox diet with increasing temperature (Fleming et al. 2021). However, we found no support for our predictions of relationships between invertebrate FO in fox diet and temperature. Our results suggest that the consumption of small and large mammals and birds by foxes decreases with increasing temperature. This contrasts with results at the continental level in Australia, where the occurrence of mammals (total of all taxa) in fox diet increases with increasing temperature (Fleming et al. 2021), and in the Iberian Peninsula where the occurrence of lagomorphs in fox diet increased with increasing temperature (Díaz-Ruiz et al. 2013). This suggests that there may be continent-specific relationships between some biogeographical variables and the dietary occurrence of specific food categories, which warrants further investigation in future studies.

Our results also suggest that the consumption of birds by foxes decreases with increasing precipitation. This could be explained by a reduction in the abundance of the main bird families consumed by foxes (Passeridae and Columbidae; Serafini & Lovari 1993, Contesse et al. 2004, Balestrieri et al. 2011), but further studies are needed to identify the precise drivers of change.

Anthropogenic impacts

Foxes can benefit from living in highly modified areas (Stepkovitch et al. 2019). At the global level, fox home range size shows a strong negative relationship with human population density (Main et al. 2019), probably because foxes benefit from food subsidies in urban areas (Bateman & Fleming 2012, Dawson et al. 2016). Nevertheless, we found no support for our prediction of a relationship between overall fox diet richness and HFI. This accords with Gámez et al. (2020), who found that diet richness of vertebrate predators is unrelated to HFI. At the European level, however, annual fox diet diversity increases with HFI, although this was not replicated during all seasons and was related to the spatial scale used to assess HFI (Soe et al. 2017).

We found that large mammal FO in fox diet decreased with increasing HFI, while bird and fruit FO increased. The increase in consumption of large mammals by foxes away from highly anthropogenic areas is likely to be due to the greater presence of wild (Underwood & Kilheffer 2016) and domestic (i.e. livestock) large mammals away from cities and built-up areas. Foxes can consume juveniles of large domestic mammals (Saunders et al. 1993, Gentle 2006) and adults when they are vulnerable (e.g. when giving birth), but large wild and domestic mammals are most likely to be taken as carrion (Catling 1988, Fleming et al. 2016).

In highly modified areas such as cities, anthropogenic features influence diversity and relative richness of birds (Aronson et al. 2014). Our results suggest that the proportion of birds in the diet of foxes increases with increasing HFI, probably as a consequence of the greater abundance of some birds closer to cities (Clergeau et al. 1998). In addition, the increase in bird prey in cities and built-up areas could reflect the greater vulnerability of ground-foraging or ground-roosting birds (Woinarski et al. 2021), increased road strike of birds around cities (Fleming et al. 2021), or common incidence of waterbirds around towns.

The increase in fruit consumption by foxes with increasing HFI is likely to be due to the abundance of horticultural, ornamental, and pest plant species around cities and built-up areas. Fruit is consumed by foxes in Europe, North Africa, and Australia (Doncaster et al. 1990, Dell'Arte & Leonardi 2005, 2009, Rosalino & Santos-Reis 2009), and foxes are effective seed dispersal agents in natural habitats (Koike et al. 2008, Rosalino et al. 2010). In anthropogenic habitats such as agricultural landscapes, consumption by foxes of domestic fleshy fruit (e.g. figs, grapes, melons, apples, olives, and cherries; Lowe 1989, Dawson et al. 2016) also makes them a potential disperser of those domestic plant species. Knowledge about the seed dispersal role of foxes in anthropogenic habitats,

especially in urbanised ones where ornamental and pest plant species are present (McKinney 2006), could be used to determine the role of foxes in the invasive potential of these plant species.

Influence of sampling methods

Digestibility of different food types taken by the fox varies considerably, which influences the results of diet composition analyses. For mammal prey, there is a direct relationship between prey body size and digestibility (Ferreras & Fernandez-de-Simon 2019). Therefore, the detected occurrence of larger mammals in diet samples derived from scats could be lower than in those derived from stomachs, and the opposite could be true of small mammals. In the present study, small and medium-sized mammals had lower FO in studies that analysed stomach contents rather than scats, while large mammals had greater FO in studies that analysed stomach contents. These findings support continental-scale results in Australia (Fleming et al. 2021). It is likely that foxes consuming small and medium-sized mammals eat a greater proportion of solid parts (e.g. bones and hairs, which are indigestible) than those consuming large mammals. We also found greater FO of fruit in studies that analysed scat contents rather than stomachs. This could also reflect the fact that some authors failed to consider fruit as possible dietary item for foxes (Brunner et al. 1975, Kirkwood et al. 2000, Rosalino & Santos-Reis 2009, Dawson et al. 2016). For instance, in our dataset 17% of studies based on stomachs and 10% of studies based on scats did not report data for fruits. Indeed, contrary to our result, Fleming et al. (2021) found that plant material (including fruits and other vegetation parts) in Australian fox diets was more often recorded in studies using stomach contents than in studies based on scat analysis, probably due to the presence of highly digestible plant material (i.e. fruit pulp). Consequently, when possible, fruits should be considered as a distinct food category, separate from other vegetation parts, in order to improve the evaluation of any temporal (seasonal) variation or spatial variation (e.g. related to the distribution of cultivated and wild fruiting plants).

CONCLUSIONS

1. This study confirms the high dietary plasticity of foxes at a global scale, but with a general trend for small mammals and invertebrates to be the most frequently occurring dietary items.
2. Changes in the FO of food categories in fox diet with geographic factors (latitude and elevation) and climatic factors (temperature and precipitation) suggest that their feeding behaviour is spatially adaptive to prey/food availability.
3. The influence of HFI on large mammal, bird, and fruit FO in fox diet highlights the opportunistic feeding behaviour of foxes. Their ability to exploit novel anthropogenic food resources such as orchard fruit makes foxes one of the most successful mammalian species in highly anthropogenic habitats.
4. Climatic factors such as temperature and precipitation influence fox diet richness. In particular, fox diet richness decreases with increasing temperature and precipitation. These results suggest that fox diet composition can become more specialised or shift, in accordance with climatic factors.
5. Sampling method influences the FO of mammals and fruit in fox diet, which suggests a need for standardised approaches to characterise fox diets in future studies.

FUNDING

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Data extraction procedure.
Appendix S2. List of studies included in this review.
Appendix S3. Effects of the anthropogenic variable HFI (Human Footprint Index) on frequency of occurrence (%) of food categories estimated by generalised linear models.
Appendix S4. Data used in the analyses.

Appendix S5. Mean ± 95% confidence intervals (CI) of frequency of occurrence (%) of food categories in red fox diet, globally and in the five continents.

Appendix S6. Boxplots of among-group and within-group dissimilarities in red fox diet.

Appendix S7. Parameter estimates and standard errors from the best latitude generalised linear models to describe variation in frequency of occurrence (%) of food categories in red fox diet.

Appendix S8. Parameter estimates and standard error from the best temperature generalised linear models to describe variation in frequency of occurrence (%) of food categories in red fox diet.

Appendix S9. Effect of temperature models, including significant climatic variables on dietary richness estimated by generalised linear models.

Appendix S10. Effects of temperature models, including significant geographic, climatic, anthropogenic, and type-of-sample variables, on frequency of occurrence of food categories estimated by generalised linear models.