Research in Veterinary Science 202 (2026) 106064

Contents lists available at ScienceDirect

Research in Veterinary Science

journal homepage: www.elsevier.com/locate/rvsc

Epidemiological factors of *Eucoleus aerophilus* infection in red foxes (*Vulpes vulpes*) from semi-arid Mediterranean environments

I. Arcenillas-Hernández [a,1], M. Català-Barrasetas [a,1], P. Pérez-Cutillas [b,*], M.R. Ruiz de Ybáñez [a], C. Martínez-Carrasco [a]

[a] *Dpto. de Sanidad Animal, Facultad de Veterinaria, Universidad de Murcia, 30100 Espinardo, Murcia, Spain*
[b] *Dpto. de Geografía, Facultad de Letras, Universidad de Murcia, 30001 Murcia, Spain*

ARTICLE INFO

Keywords:
Eucoleus aerophilus
Parasite
Red fox
Respiratory nematodes
Semi-arid area
Environment

ABSTRACT

Eucoleus aerophilus is a ubiquitous zoonotic nematode found in the tracheobronchial mucosa of the definitive hosts, described in wild and domestic canids, including the red fox (*Vulpes vulpes*). To assess *E. aerophilus* occurrence and intensity in red foxes, the respiratory system of 126 foxes from Region of Murcia (SE, Spain) were examined. Statistical analyses were performed to investigate the influence of biotic and abiotic factors on the parasite's occurrence. The occurrence of *E. aerophilus* was 28.6% (95% CI: 20.6–36.4), with a mean intensity of 3.1 nematodes per parasitised fox. The infection rate and parasite intensity were higher in forested areas, suggesting that earthworm abundance and a longer survival of infective *E. aerophilus* eggs increase the risk of transmission and maintenance in the environment. Moreover, an inverse relationship between *E. aerophilus* occurrence and temperature ($p < 0.05$) was observed. Results demonstrated that foxes participate in maintaining the cycle of *E. aerophilus* in semi-arid Mediterranean environments. This should be taken into account at the wild-domestic-human interface. The development of a predictive model of *E. aerophilus* infection risk in red foxes will allow the design of future strategies for the prevention of capillariosis, especially in areas where contact between foxes, domestic carnivores, and humans exists.

1. Introduction

Eucoleus aerophilus (synonym: *Capillaria aerophila*) is a nematode belonging to the family Capillariidae (Nematoda; Trichocephalida; superfamily Trichinelloidea). Capillariidae family contains a diverse group of genera, including *Eucoleus* spp., which are parasites that affect the respiratory system of mammals and, in birds, the esophagus, oral cavity, and stomach (Tamaru et al., 2025). In the *Eucoleus* genus, males are characterised by lateral alae and a pseudobursa, which is formed by two small, rounded lobes directed towards the posterior. They also have slender spicules surrounded by a long, spine-covered spicular sheath. Females possess a vulva with a cuticular appendage, and the eggs they lay have a porous shell. The life cycle of *E. aerophilus* is still unclear; some researchers suggest that it has a direct life cycle (through ingestion of embryonated eggs), while others propose that it may be indirect, with earthworms possibly acting as intermediate or paratenic hosts (Anderson, 2000; Traversa et al., 2010; Di Cesare et al., 2014; Samorek-Pieróg et al., 2023). This cosmopolitan nematode is associated with significant respiratory disease in both wild and domestic canids and felids, including red foxes (*Vulpes vulpes*) (Di Cesare et al., 2014; Tolnai et al., 2015; Schug et al., 2018; Samorek-Pieróg et al., 2023; Polotzek et al., 2025). Moreover, cases of pulmonary capillariosis have been reported in humans from different countries worldwide (Aftandelians et al., 1977; Laloševic et al., 2008).

The red fox is a wild carnivore known for its adaptability, generalist behaviour and worldwide distribution, which presence is favored by the availability and abundance of food, as well as by patchy habitats (Gortázar, 2007). Foxes feed on a wide variety of resources including invertebrates, fruits, seeds, small mammals, reptiles, carrion and anthropogenic refuses (Díaz-Ruiz et al., 2013; Soe et al., 2017). This dietary plasticity, coupled with the abundant food availability in peri-urban and urban areas, has led to an increase of fox populations in these environments (Gloor et al., 2001; Contesse et al., 2004). In this sense, diet may significantly influence the helminth community in foxes,

* Corresponding author.
E-mail address: pedrope@um.es (P. Pérez-Cutillas).
[1] These authors contributed equally to this work.

https://doi.org/10.1016/j.rvsc.2026.106064
Received 26 October 2025; Received in revised form 21 December 2025; Accepted 11 January 2026
Available online 13 January 2026

since many of these parasites, including cardiopulmonary nematodes like *E. aerophilus*, have indirect life cycle involving trophic transmission (Eira et al., 2006; Lalošević et al., 2013; Magi et al., 2015; Hodžić et al., 2016). On the other hand, environmental heterogeneity, land use variations and territory fragmentation influence fox population densities (García et al., 2009; Gortázar, 2007). Given the effective adaptative and dynamic response of fox populations to these factors, the increasing presence of foxes in urban, peri-urban and rural areas can heighten the risk of pathogen transmission at the wild-domestic-human interface (Otranto and Deplazes, 2019).

In a recent study, a high occurrence of *E. aerophilus* (26.9%) was found in the fox population of southeastern Spain (Arcenillas-Hernández et al., 2024), though it did not examine the environmental factors that might be determining the parasite's spread. So, given the limited understanding of *E. aerophilus* epidemiology, the factors influencing its spread and distribution remain largely undetermined (Traversa et al., 2010). Closing this knowledge gap and preventing future *E. aerophilus* spread requires a comprehensive approach that implements surveillance focused on key host species in the parasite's life cycle (Eira et al., 2006; Martínez-Carrasco et al., 2007), understanding fox population dynamics and the environmental conditions affecting parasite transmission. Sustained, long-term monitoring of these factors is crucial for effective control (Franssen et al., 2014; Tolnai et al., 2015).

Considering the complex interaction of variables in parasite-host systems, the aims of this study were (i) to elucidate the biotic and abiotic factors that could influence the distribution, occurrence and intensity of *E. aerophilus* in foxes inhabiting semi-arid Mediterranean areas of the Iberian Peninsula, and (ii) to identify areas with the highest predicted epidemiological risk of *E. aerophilus* infection.

2. Material and methods

2.1. Study area and sample collection

The study area includes the territorial boundaries of the Region of Murcia (SE, Spain), an area with semi-arid Mediterranean climate where annual precipitation is less than 350 mm, and that presents high average annual temperatures and significant levels of evapotranspiration (Miró et al., 2018).

From 2015 to 2020, a total of 126 cardiorespiratory system were obtained from foxes (71 males and 55 females) originated from hunting programmes, wildlife recovery centres or roadkill incidents. Foxes included in this study were a subset of those examined in a recent investigation on the presence of cardiopulmonary and gastrointestinal nematodes in foxes (Arcenillas-Hernández et al., 2024). The primary selection criterion was the availability of complete data on the foxes' geographical origin. Necropsies were performed at the Animal Health Department (University of Murcia). Foxes were classified as juveniles (4 individuals, <12 months old), subadults (39 individuals, 12–24 months) and adults (83 foxes, >24 months), based on Sáenz de Buruaga et al. (1991). To estimate the body condition of foxes, the Kidney Fat Index (KFI) was calculated according to Riney (1955) and Winstanley et al. (1998). Following extraction, thoracic viscera of each fox were placed into labelled plastic bags and frozen at −20 °C until further analysis.

2.2. Isolation and identification of nematodes

Thoracic viscera were analysed according to Arcenillas-Hernández et al. (2023). Firstly, each cardiorespiratory system was longitudinally opened through the tracheobronchial tree and the large pulmonary vessels. Trachea and heart were washed and filtered using a sieve (mesh diameter 63 μm); and the opened pulmonary parenchyma was observed under stereomicroscope. Subsequently, lung parenchyma was cut (3 × 3 cm pieces) and squeezed in water, and the content was filtered and examined under the stereomicroscope. Finally, due to the possible presence of nematodes in bronchi of smaller diameter, the pieces of lung parenchyma were artificially digested as described by Martínez-Rondán et al. (2019). Briefly, samples were immersed in a pepsin-chlorohydric acid (1.5%) solution, subjected to constant agitation at 40 °C for 15 min. Once again, the remaining content was observed under the stereomicroscope. Nematodes recovered from the previously described phases were washed and preserved in absolute ethanol until morphological identification according to Anderson et al. (2009) and Lalošević et al. (2013).

2.3. Analysis of environmental data

To characterize the habitat of the foxes, environmental variables were extracted from the home ranges of 116 individuals (10 individuals were not tracked by coordinates) (Fig. 1). The geographic coordinates of each fox' s origin was recorded to create a geospatial database. The average size of the fox home range was estimated to be 400 ha, based on a 1.13 km radius, consistent with previous studies such as Deak et al. (2020).

Environmental data were analysed using the Geographic Information System (QGIS v.3.28). The ASTER Global Digital Elevation Model (GDEM) was used, providing a base resolution of 15 m per pixel (ASTER GDEM V3, 2018). From this data, the mean, maximum and minimum altitude of each home range were obtained, and based on these data, the home range of each fox was calculated. Climate data, including mean, maximum, and minimum temperature, precipitation, and solar radiation, were obtained from the Digital Climate Atlas of the Iberian Peninsula (Ninyerola et al., 2005).

Both human population densities and the distance from the locations where foxes were found to the nearest localities with populations exceeding 3000, 5000 and 10,000 inhabitants/km^2 were calculated using Spanish census data (INE, 2020). Land cover data were obtained from the Fourth National Forest Inventory (MITECO, 2024), which provides a detailed and standardised classification of land surfaces based on vegetation type, structure and land use. The classification system is hierarchical, distinguishing main land cover categories such as forest areas (45.1% of the study area), agricultural areas (49.4%), artificial areas (5.1%), water areas (0.3%), and wetlands (0.1%), which are further subdivided into subcategories and specific subclasses. Specifically, forest areas are particularly well characterised and are of special relevance in Mediterranean ecosystems. In the semi-arid southeast of the Iberian Peninsula, the native forest subclass refers to natural stands dominated by drought-adapted autochthonous species such as *Pinus halepensis*, *Quercus coccifera* and scattered individuals of *Tetraclinis articulata*, often forming open woodlands with sparse canopy cover and a xerophytic understorey. Gallery forests (riparian woodlands), although scarce and fragmented in this region, are associated with watercourses and characterised by species such as *Populus alba*, *Tamarix* spp. and *Nerium oleander*, forming narrow linear formations with high ecological sensitivity. Plantation forests are generally composed of monospecific stands of *Pinus halepensis* or *Pinus pinea*, occasionally *Eucalyptus* spp., primarily established for reforestation, erosion control or productive purposes, and typically lacking structural heterogeneity. The inventory further distinguishes residual woodland fragments (<6 ha) and small forest patches (<20 ha), which represent isolated or discontinuous remnants of forest vegetation, often embedded within agricultural or degraded landscapes and subject to edge effects. This level of thematic resolution enables precise ecological characterisation of forest habitats, facilitating robust spatial analyses in both environmental and epidemiological contexts.

2.4. Statistical analysis

Infection rate, median abundance and median parasite intensity of *E. aerophilus* were calculated according to Margolis et al. (1982) and Bush et al. (1997). To study the statistical relationships between sex, age or body condition and the occurrence, Fisher test was performed, and in

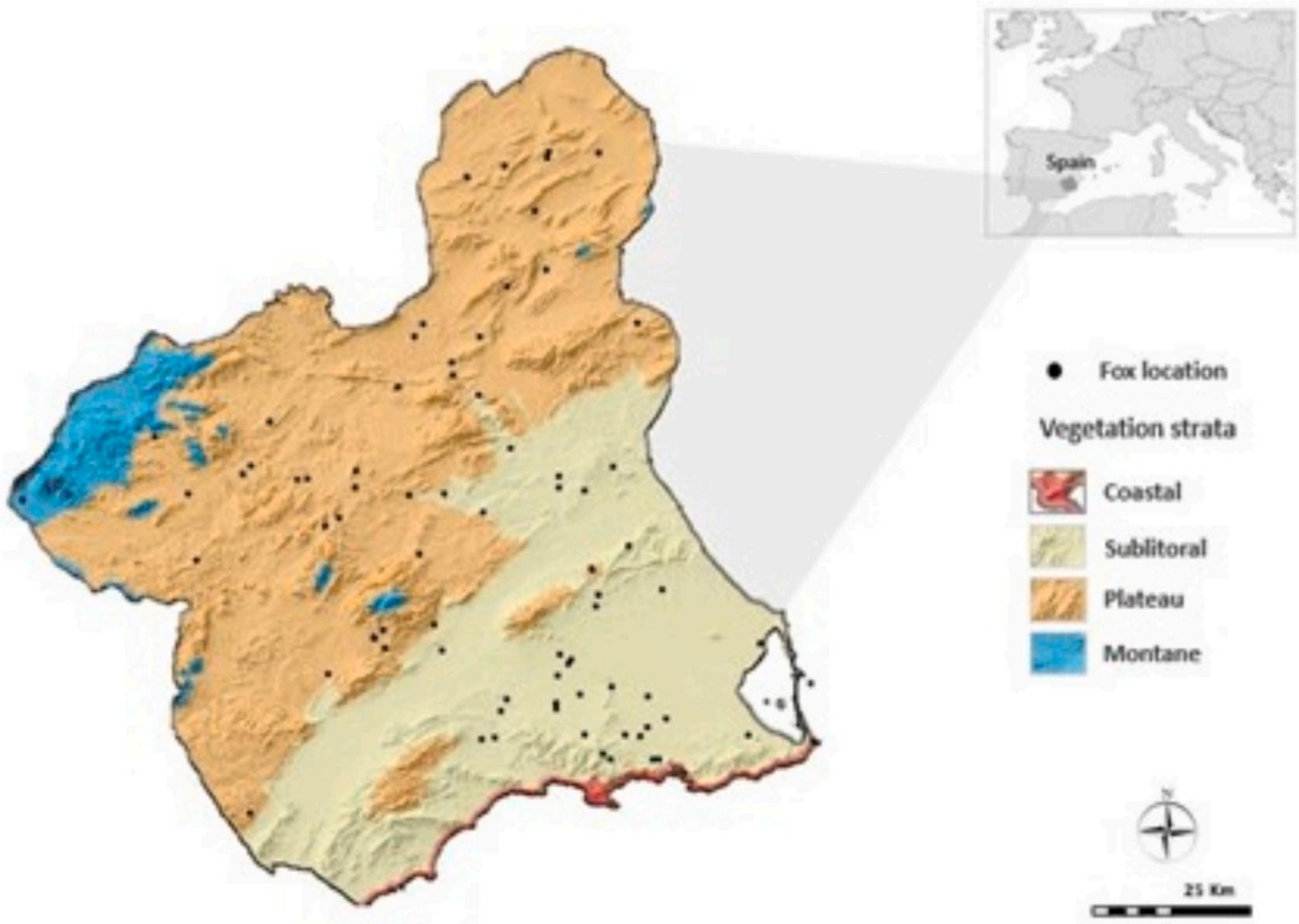

Fig. 1. Distribution of the vegetation floors in the Region of Murcia according to Alcaraz et al. (2008). Dots in black correspond to the location where foxes were collected.

case of parasite intensity, the Kruskal-Wallis test was used. The influence of KFI, environmental variables, land uses, land cover and the human density effect were analysed using the Kruskal-Wallis test for the occurrence, and Kendall rank correlation coefficient for parasite intensity. Spearman correlation coefficient was calculated in case of variables with a p-value <0.1. For carrying out statistical analysis, R software 4.2.0 (R Core Team, 2024) was used, and significance threshold was established for p value <0.05. For this purpose, functions from R's base "stats" package were used to perform linear modeling (lm), correlation analyses (cor.test), and non-parametric tests (kruskal.test, ks.test). In addition, the MASS package (Venables and Ripley, 2002) was employed for automatic model selection using the Akaike Information Criterion (AIC).

The difference between parasite intensity of this study and the observed by Martínez-Carrasco et al. (2007) was tested with one-sample *t*-test. Finally, a predictive model of the infection risk of *E. aerophilus* based on the parasite intensity and the mean temperature was carried out with the program Past v.3. By applying the analysis of environmental variables and the results of the predictive model, a normalized risk map of infection was created using QGIS V.3.28 (QGIS Development Team, 2024), which spatially displayed the information.

3. Results

The occurrence of *E. aerophilus* was 28.6% (36/126 foxes; 95%CI: 20.6–36.4), with infected individuals harbouring a mean intensity of 3.1 nematodes, and a maximum of 15 nematodes in a single host (Table 1). The distribution of *E. aerophilus* in infected foxes showed a pattern of parasite aggregation; specifically, most foxes harboured only 1–2 nematodes (20/36; 55.6%), 13 foxes had 3–6 nematodes (13/36; 36.1%), and only three individuals (8.3%) were found with 8, 10 and 15 nematodes, respectively.

Spatial variables also influenced parasite occurrence. Occurrence was higher at lower longitudes, while a positive trend was observed with increasing latitude and altitude, although these relationships showed marginal statistical significance (Figs. 2; 3). In addition, parasite occurrence tended to increase with greater distance from human settlements with population densities exceeding 5000 inhabitants/km^2, suggesting a higher prevalence in less anthropised areas (Fig. 2).

The occurrence of E. aerophilus was significantly associated with climatic variables, particularly mean and minimum temperature. In both cases, higher temperatures were linked to a lower probability of parasite occurrence, indicating a negative relationship between thermal conditions and the infection exposure risk (Table 2; Fig. 4).

Land-use and land-cover variables showed clear effects on parasite occurrence. The highest values of presence were associated with forested areas, including wooded forests, forest plantations, and mosaics of scrub/grassland with bare soil. These types of land cover consistently favored the presence of E. aerophilus, particularly with small forest plots (<20 ha) (Table 3), whereas a negative relationship was observed with infrastructures linked to the primary sector. Conversely, areas characterised by a greater extent of waste-related infrastructures (e.g. landfills,

Table 1
Infection rate (95% CI), median intensity, and range of *E. aerophilus* in foxes from southeast Spain ($n = 126$).

Variables	Levels	n	n positives	Occurrence (95% CI)	Median intensity	Range
Age	12 months	4	0	0 (0–0)	0	0
	12–24 months	39	5	12.8% (2.33–23.31)	4.40	2–10
	> 24 months	83	26	31.3% (21.35–41.30)	2.85	1–15
Sex	Female	55	13	23.6% (12.41–34.86)	2.23	1–8
	Male	71	23	32.4% (21.51–43.28)	3.52	1–15

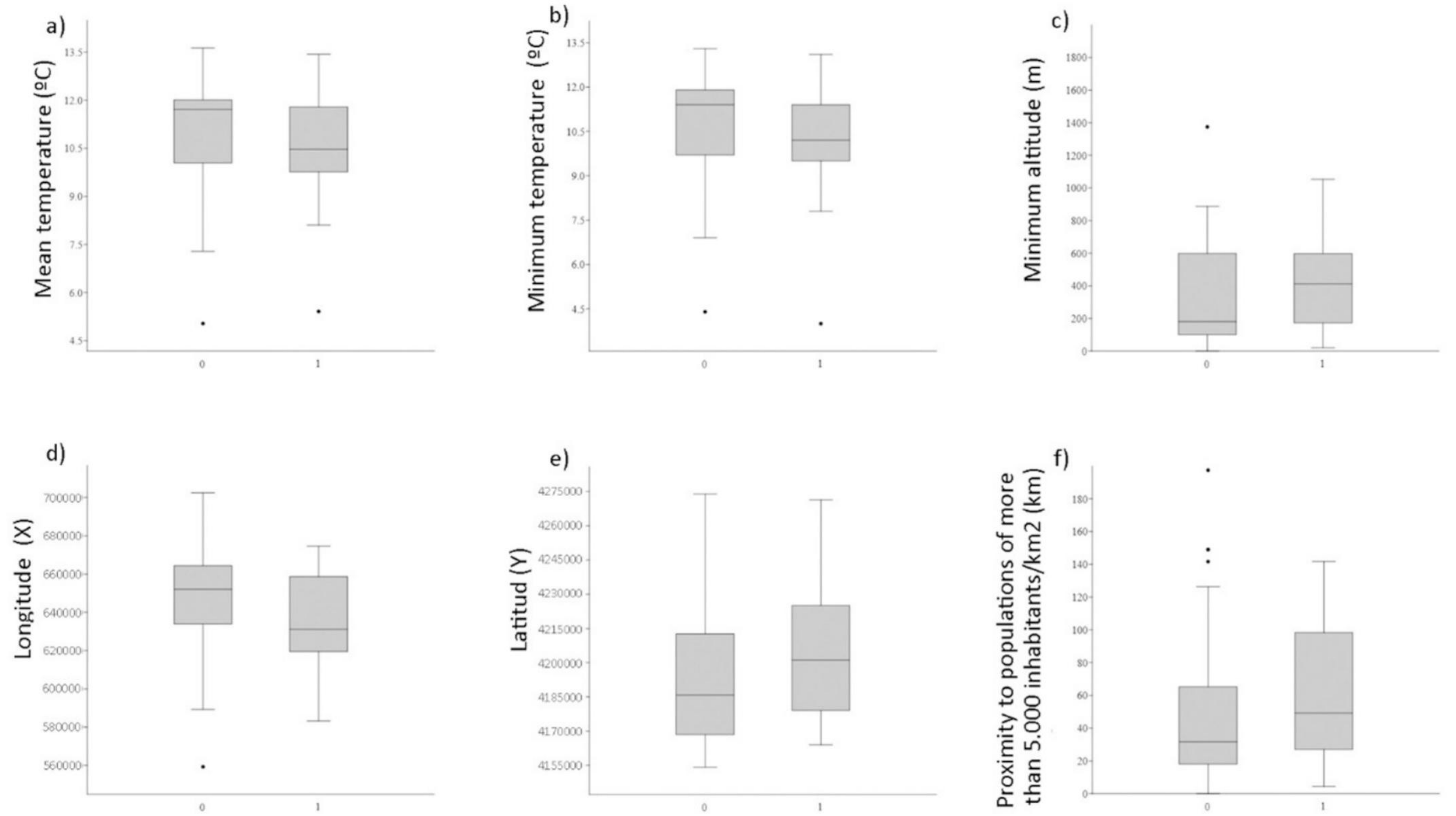

Fig. 2. Results obtained for the absence (0) and presence (1) of *E. aerophilus* in relation to mean temperature (a), minimum temperature (b), minimum altitude (c), longitude (d), latitude (e) and proximity to populations of more than 5.000 inhabitants/km^2.

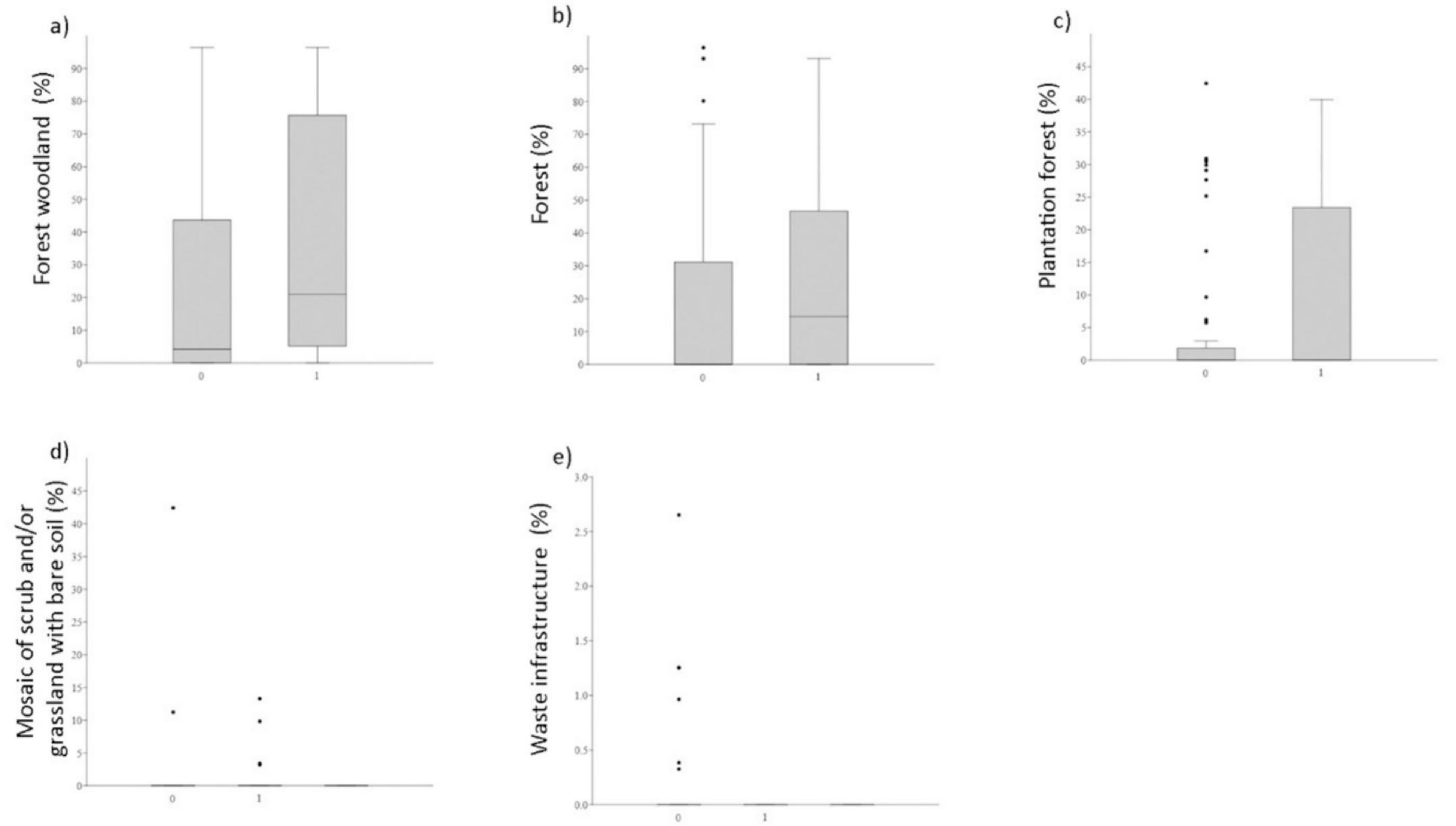

Fig. 3. Results obtained according to the absence (0) and presence (1) of *E. aerophilus* in relation to the area of forest woodland (a), forest (b), plantation forest (c), mosaic of scrub and/or grassland with bare soil (d) and waste infrastructure (e).

dumps, and treatment plants) showed lower occurrence values, although this relationship was marginally significant. In addition,

Table 2
Statistical analysis of *E. aerophilus* occurrence and mean intensity in foxes by host variables, season and year (n = 126), and environmental variables (*n* = 116).

Variable	p-value occurrence	p-value parasite intensity
Host age category (<12 months; 12–24 months; >24 months)	0.3548	0.4775
Host age category (<24 months; >24 months)	0.4577	0.4775
Sex	0.3786	0.103
Body condition	0.3332	0.2094
KFI (%)	0.8443	0.676
Weight	0.346	0.888
Maximum temperature	0.3211	0.4117
Mean temperature	0.02392*	0.01899*
Minimum temperature	0.03159*	0.01966*
Radiation	0.8543	0.4796
Annual precipitation	0.5047	0.2345
Reference evapotranspiration	0.4443	0.5415
Maximum altitude	0.1022	0.718
Mean altitude	0.1075	0.289
Minimum altitude	0.09535**	0.718
Altitude range	0.1976	0.08555**
Season	0.8468	0.309
Year	0.3726	0.04015*
Longitude (X)	0.04216*	0.3192
Latitude (Y)	0.05699**	0.001047*
Human density	0.8725	0.3522
Distance to the nearest human settlement	0.6118	0.3706
Distance to the nearest population with density > 10,000 inh/km^2	0.1172	0.9232
Distance to the nearest population with density > 5000 inh/km^2	0.08659**	0.4599
Distance to the nearest population with density > 3000 inh/km^2	0.1986	0.936

parasite intensity decreased with increasing extent of discontinuous urban areas, indicating lower parasite burdens in more urbanised landscapes (Table 3; Fig. 5).

Parasite intensity was also influenced by the temporary factor, showing an increase during the study period and revealing a positive temporal trend in infection load (Table 2). A marginal effect of host sex was also observed, with males harbouring a higher mean parasite burden than females (Table 1).

Finally, a spatial prediction model for *E. aerophilus* intensity was generated based on the effect of mean temperature, the variable showing the strongest and most consistent association with parasite burden. The resulting model, illustrated in Fig. 6, predicts higher parasite intensities under lower mean temperature conditions. The predictive relationship is described by the following equation:

$$Intensity = 10\hat{}(-0.0211^{*}\ \text{Mean temperature} + 3.21)$$

This model provides a spatially explicit representation of areas with a higher expected parasite burden and serves as a basis for interpreting the environmental drivers underlying the observed epidemiological patterns.

4. Discussion

This study demonstrates that *E. aerophilus* is a widely spread parasite in foxes inhabiting semi-arid Mediterranean areas, with a prevalence of 28.6% and a mean intensity of 3.1 nematodes per infected host. Parasite aggregation was evident in the distribution of *E. aerophilus* among infected foxes, aligning with the typical observation for nematodes where a few hosts carry most of the parasites within a potential host population (Poulin, 2007; Gourbière et al., 2015). Moreover, the occurrence of this multi-host nematode was significantly linked to environmental and land-use factors, underscoring the strong influence

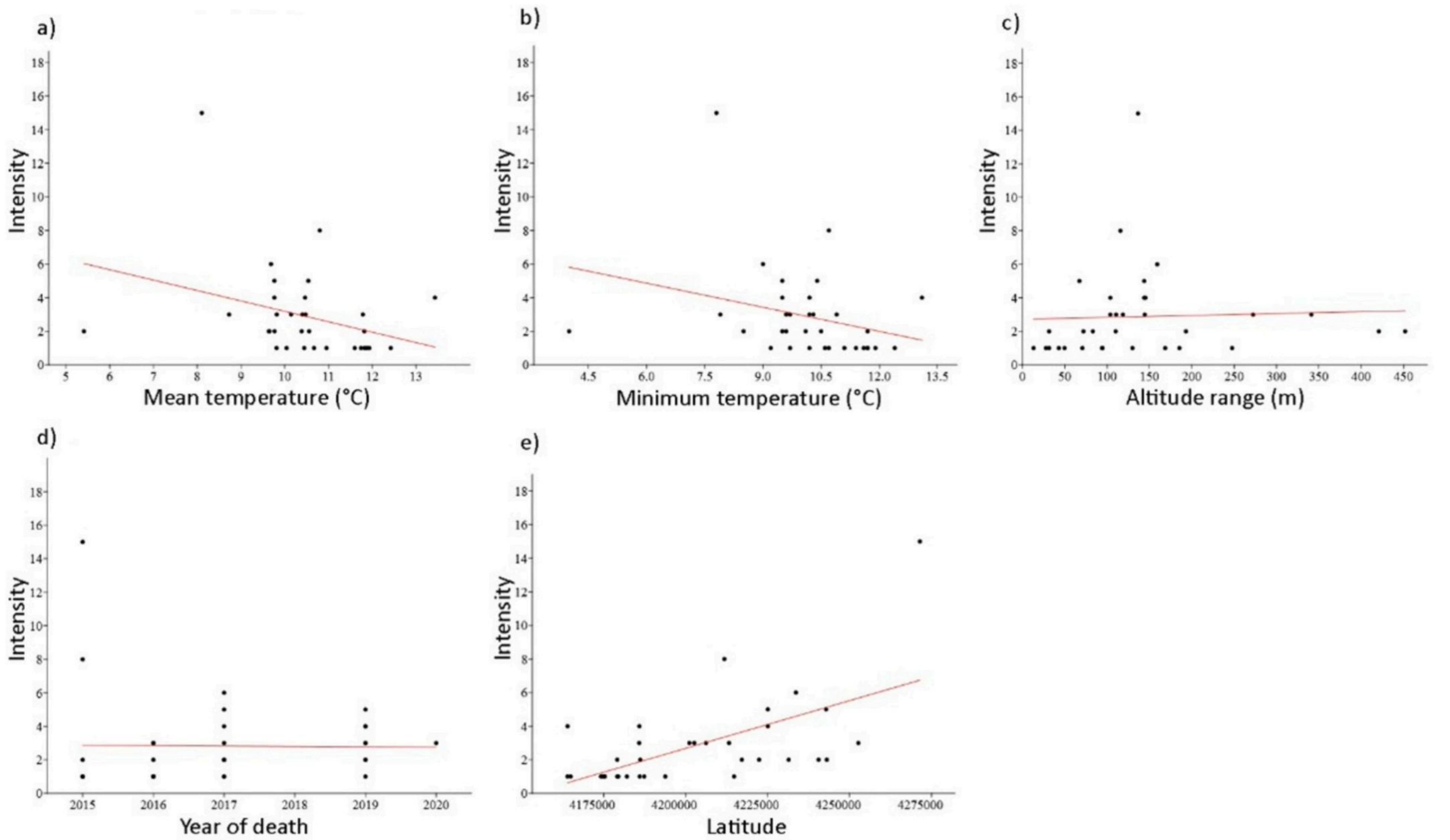

Fig. 4. Intensities of *E. aerophilus* obtained as a function of mean temperature (a), minimum temperature (b), altitude range (c), year of death (d) and latitude (e). The red mark shows the trend line of the analysed series. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
P-value results for the occurrence and intensity of *E. aerophilus* for different land-use types based on the home range of the studied foxes (n = 116).

Land use	Main category	Subclasses	p-value (occurrence)	p-value (intensity)
Forest areas			0.2653	0.6761
	Forested woodland		0,02313*	0.2206
		Forest	0,05783**	0.2583
		Gallery forest	0.4991	0.4539
		Plantation forest	0,04795*	0.6778
		Forest patches (<20 ha)	0.6555	0,01055*
	Firebreaks		0.3705	NA
	Herbaceous vegetation		0.9322	0.8605
		Herbaceous-pasture mix	0.9159	0.8605
		Pasture with crops and/or meadow mosaic	0.5283	NA
	Shrubland		0.7479	0.4261
		Bushy formations	0.9827	0.4427
		Shrubland with scattered trees	0.2706	NA
		Shrubland and/or pasture with bare soil mosaic	0,03673*	0.3062
		Pasture-shrub mix	0.2795	0.3237
		Residual forest (<6 ha)	0.9199	1
	Patches with sparse or no vegetation		0.1514	NA
		Beaches, dunes and sandy areas	0.2706	NA
		Sea cliffs	0.5283	NA
		Rock outcrops	0.5283	NA
		Eroded areas	0.5283	NA
Agricultural surfaces			0.4156	0.6072
	Croplands		0.4553	0.6072
		Crop-artificial land mosaic	0.6391	NA
		Crop with shrubland and/or herbaceous mosaic	0.2583	NA
Artificial surfaces			0.6391	0.3023
		Facilities / Institutional uses	0.1636	0.3483
		Industrial	0.8194	0.335
		Energy infrastructure	0.8999	0.2544
		Waste infrastructure	0,08679**	NA
		Water supply infrastructure	0.85	0.2544
		Transport infrastructure	0.6488	0.493
		Primary sector	0.6785	0,02156*
		Tertiary sector	0.5592	0.2349
		Continuous urban fabric	0.3543	0.2896
		Discontinuous urban fabric	0.1992	0,07288**
		Other artificial surfaces	0.71	0.5549
Water surfaces			0.3746	0.609
	Wetlands: Coastal wetlands		0.5283	NA

* p < 0,05; **p < 0,1.

of these factors on the *E. aerophilus* life cycle maintenance and, consequently, its potential spread.

Studies across Europe reveal a wide variability in *E. aerophilus* prevalence in red foxes, ranging significantly from 4.7% in Croatia to 97.1% in Lithuania (Table 4).

These differences could be explained by several factors, such as environmental characteristics, or the diagnostic technique used (Nevárez et al., 2005; Lalošević et al., 2013), with coprological techniques and necropsy being the most common (Samorek-Pieróg et al., 2024). In our study, necropsy was used for parasite detection following a rigorous protocol that reduces the risk of false negatives (Arcenillas-Hernández et al., 2023); consequently, we are confident the detected infection rate is not underestimated, which might have happened if we had relied solely on coprological techniques to detect *E. aerophilus* eggs.

The influence of host variables (age and sex) on the presence of *E. aerophilus* in foxes has been explored in previous studies, revealing divergent results (Martínez-Rondán et al., 2019; Deak et al., 2020). Consistent with other studies (Davidson et al., 2006; Hodžić et al., 2016; Martínez-Rondán et al., 2019), our study similarly found no relationship between the prevalence and host variables. On the other hand, while Lindenfors et al. (2007) indicated a significant correlation between the body mass and diet of carnivores with parasite species richness, this study explored a similar premise for foxes in semi-arid Mediterranean areas. Consequently, this study aimed to determine whether fox body condition, KFI and weight could serve as reliable proxies for the risk of being parasitised by *E. aerophilus*. Nevertheless, our findings did not provide significant differences in prevalence and parasite intensity related to these variables.

In terms of host sex, our results indicate that fox males tend to have higher parasite intensity than females ($p = 0.103$), as previously noted Martínez-Rondán et al. (2019) in foxes from the northwest Iberian Peninsula. It has been suggested by various authors that the greater susceptibility observed in males might be due to a trade-off mechanism between sex hormones (testosterone) and the immune response, as proposed by various authors in different mammalian host species (Folstad and Karter, 1992; Decristophoris et al., 2007). However, this hypothesis (referred to as the immunocompetence handicap hypothesis) remains controversial (Roberts et al., 2004).

Regarding environmental variables, the results of this study showed that increases in mean temperature and minimum temperature are related with a decline in both the infection proportion and intensity of *E. aerophilus*. In this sense, other authors have also reported this relationship between occurrence and temperature (Tolnai et al., 2015; Martínez-Rondán et al., 2019). In addition, the results suggested a rise in the occurrence with an increasing minimum altitude of the fox home range. This observation agrees with Tolnai et al. (2015), Martínez-Rondán et al. (2019) and Deak et al. (2020), who also detected a positive correlation between *E. aerophilus* prevalence and altitude. However, it should be considered that altitude itself might not be the direct cause. Instead, the decrease in temperature that typically accompanies higher altitudes is probably the key factor promoting the parasite presence, particularly in semi-arid Mediterranean areas. In this regard, Segovia et al. (2004) carried out a study in mountainous areas of the Iberian Peninsula and attributed the higher *E. aerophilus* prevalence to a greater abundance of earthworms in those elevated habitats; this would increase the probability that these intermediate hosts of *E. aerophilus*, becoming part of the diet of foxes. In addition, environmental factors, including temperature and relative humidity, are crucial for the spread of *E. aerophilus* as they directly impact the survival of its eggs in the environment (Traversa et al., 2011; Arcenillas-Hernández et al., 2022). This is supported by Tolnai et al. (2015), who suggested that precipitation and temperature influence the occurrence because *E. aerophilus* eggs are highly susceptible to desiccation. However, the resistance of *Eucoleuss* spp. eggs in nature is unknown (Traversa et al., 2011), although studies on the related nematode *Eucoleus böhmi* have shown that its eggs can survive and develop at 5–20 °C with 85% RH, but not

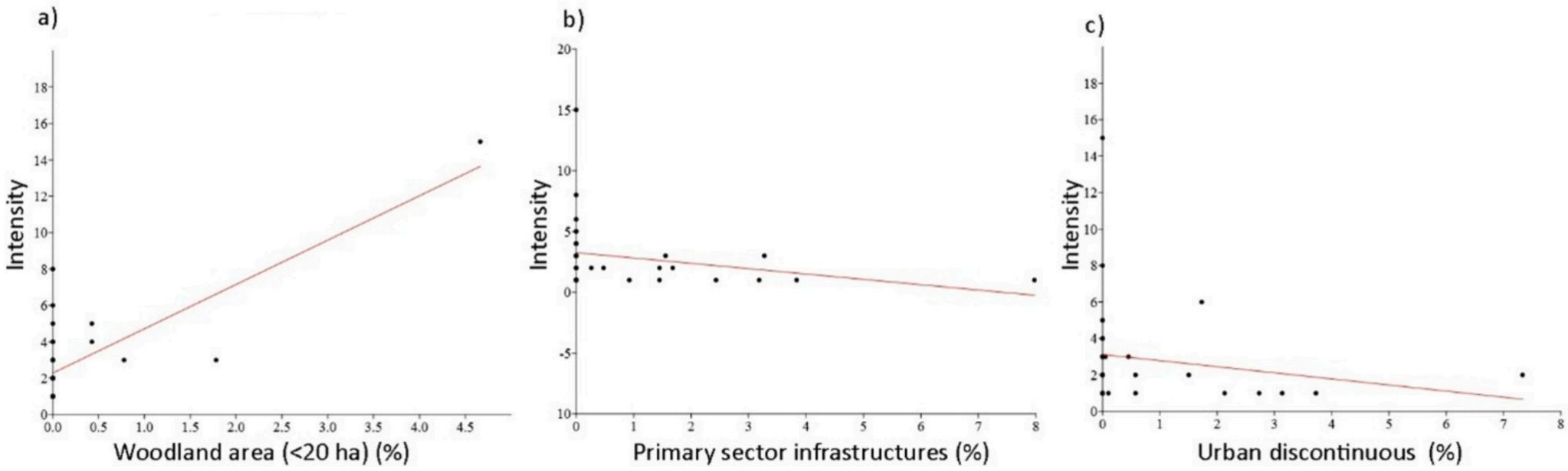

Fig. 5. Intensities of *E. aerophilus* obtained attending to the woodland area (<20 ha) (a), primary sector infrastructures (b) and urban discontinuous (c). The red mark shows the trend line of the series analysed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

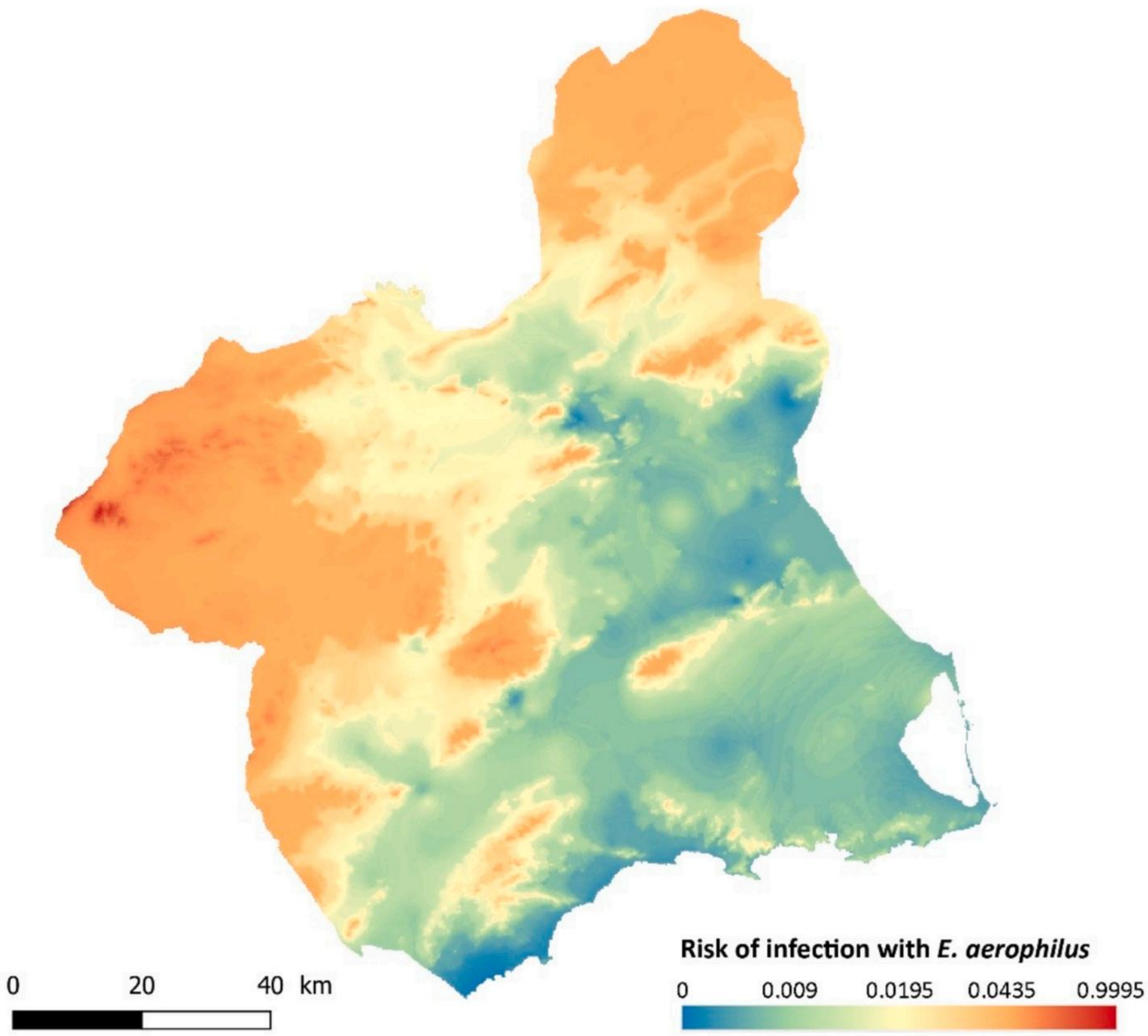

Fig. 6. Risk map of the *E. aerophilus* in the Region of Murcia (southeaster Spain).

with 45% RH (Perrucci et al., 2014). In our study, precipitation, radiation and evapotranspiration variables were used to check the effect of environmental dryness on the occurrence and intensity of *E. aerophilus*, but no significant differences were found.

In foxes inhabiting semi-arid Mediterranean areas, no seasonal influence on the occurrence and intensity of *E. aerophilus* was observed. These results contrast with those reported by Schug et al. (2018) in Germany, who observed that the prevalence of this nematode in foxes was marginally related to season, with higher prevalence in winter. This difference could be attributed to the climatic contrast between Central Europe and the semi-arid Mediterranean areas (Twardosz et al., 2021); furthermore, the availability of intermediate hosts might also play a role, as their presence largely depends on environmental conditions.

As for the territorial distribution of *E. aerophilus*, a significant rise in occurrence was detected towards the west (lower longitude). Additionally, both infection proportion and intensity increased with higher latitude (i.e., towards the north of the study area) (Fig. 6). These relationships could indirectly reflect climatic and orographic conditions, as northwester areas comprise the region's most mountainous and colder zones, in contrast to the less elevated and warmer southeast.

The presence of *E. aerophilus* was clearly influenced by land use. Our study specifically revealed a positive correlation between *E. aerophilus* occurrence and the most common forest areas in the Region of Murcia (i.e., forests and forest plantations). There was a significant relationship between the parasite intensity in foxes and the presence of small forest patches. These results suggest that wooded areas possess specific microclimate conditions that differ from those typically found in semi-arid Mediterranean environments. Concretely, the tree canopy protects from solar radiation and reduces temperature and evapotranspiration, leading to higher soil humidity; these conditions are crucial for

Table 4
Prevalence of *E. aerophilus* in red foxes from European countries, based on respiratory necropsy with morphological identification (MI), molecular confirmation (Mol), or coproscopic examination (CE) for egg detection.

Country	Prevalence (%)	Sample size	Diagnostic technique	Authors
Bosnia and Herzegovina	69.7	221	MI, Mol	Hodžić et al. (2016)
Croatia	4.7	85	MI	Rajković-Janje et al. (2002)
Denmark	36.8	68	CE	Willingham et al. (1996)
Denmark	74.1	748	MI	Saeed et al. (2006)
Denmark	89.8	118	MI	Al-Sabi et al. (2014)
Germany	69.4	569	MI	Schug et al. (2018)
Hungary	66.0	100	MI	Sréter et al. (2003)
Hungary	61.7	937	MI	Tolnai et al. (2015)
Ireland	36.7	79	CE	Wolfe et al. (2001)
Italy	14.6	42	MI	Manfredi et al. (2003)
Italy	7.0	129	MI	Magi et al. (2009)
Italy	41.8	165	MI	Magi et al. (2015)
Italy	45.1	51	MI, Mol	Nonnis et al. (2023)
Lithuania	97.1	104	MI	Bružinskaitė-Schmidhalter et al. (2011)
Netherlands	67.7	136	Mol	Franssen et al. (2014)
Norway	88.0	181	MI	Davidson et al. (2006)
Poland	76.2	344	CE	Karamon et al. (2018)
Romania	72.5	550	MI	Deak et al. (2020)
Serbia	84.0	70	MI	Lalošević et al. (2013)
Serbia	72.6	351	MI	Čabrilo et al. (2018)
Serbia	53.0	83	MI	Gavrilović et al. (2019)
Spain	59.0	251	MI	Mañas et al. (2005)
Spain	5.4	55	MI	Martínez-Carrasco et al. (2007)
Spain	33.5	257	MI	Martínez-Rondán et al. (2019)
United Kingdom	39.0	546	MI	Morgan et al. (2008)

two key factors: the survival of infective *E. aerophilus* eggs and the maintenance of earthworm populations, which are essential intermediate hosts for the spread of this pulmonary nematode (Tolnai et al., 2015; Singh et al., 2019; Arcenillas-Hernández et al., 2022). Additionally, a positive correlation was observed between the occurrence and mosaic landscape of shrubs and pastures; although these areas lack tree cover, their environmental requirements likely lead them to be situated in sufficiently humid soils, which in turn provides the appropriate conditions for the presence of earthworms.

The spread of *E. aerophilus* in sylvatic and peri-urban environments relies on suitable definitive hosts, with foxes playing a pivotal role (Samorek-Pieróg et al., 2023). Barbosa et al. (2005) found that the probability of foxes appearing in anthropized areas is influenced by human population size. Therefore, a larger fox population logically correlates with higher risks of parasite spread. Based on this, this study hypothesized that human density and distance to human populations could influence *E. aerophilus* occurrence and parasite intensity in foxes. However, only a marginal significant rise ($p = 0.087$) in occurrence was detected with increasing distance to populations of more than 5000 inhabitants/km^2. Regarding artificial surfaces of human origin, only a marginally significant correlation was found between *E. aerophilus* occurrence and waste infrastructures. Moreover, parasite intensity was correlated with rural areas dedicated to the primary sector (i.e., agricultural and livestock areas with discontinuous urban surfaces). All these findings suggest that foxes in anthropized areas have a lower probability of being parasitized. These areas are attractive to foxes because they offer a wide variety of trophic resources (Contesse et al., 2004), which likely leads to a reduction in earthworm consumption. Conversely, in areas far from urban centres or with less human activity, foxes probably must compensate for the absence of abundant and easily accessible food with other nutritional resources, including prey like earthworms. This difference in diet could be why the presence of *E. aerophilus* in foxes is not associated with highly anthropized areas.

Although co-infections with other cardiopulmonary nematodes such as *Crenosoma vulpis* (22.2%; 7/36) and *Angiostrongylus vasorum* (44.4%; 16/36) were investigated and reported in other publications derived from the same research project (Arcenillas-Hernández et al., 2024), they were not included in the present analysis. The rationale for this exclusion lies in the specific aim of this study, which was to explore the environmental determinants of *E. aerophilus* occurrence as an emerging parasite under semi-arid Mediterranean conditions.

The study on the spatial distribution of *E. aerophilus* infection risk in foxes from southeaster areas of the Iberian Peninsula provides a precise risk map that is highly relevant for other semi-arid Mediterranean areas and pivotal for understanding the spread of this pulmonary nematode, which also poses a threat to dogs, cats (Traversa et al., 2009), and even humans (Laloševic et al., 2008). For future research, we suggest developing similar risk maps that incorporate both parasite intensity and the exact geographical location of studied animals. This will allow a more robust comparison of environmental risk factors influencing the parasite spread across bioclimatic areas. Additionally, incorporating fox abundance into future spatial analyses is relevant, despite the inherent challenges of obtaining such data for wild species. In fact, host density is known to be a predictor of parasite species richness (Lindenfors et al., 2007). Therefore, integrating this variable in the study would provide key information for understanding the epidemiological dynamics of *E. aerophilus* and its potential risk to foxes and other susceptible carnivore species.

This analysis complements our previous publication (Arcenillas-Hernández et al., 2024), which provided a broader parasitological overview of cardiopulmonary and gastrointestinal nematodes in red foxes from the same region. In contrast, the present study focuses specifically on *E. aerophilus*, integrating environmental variables to identify the ecological drivers of infection and to develop a parasite-specific risk model. Finally, this study indicates an increase on the occurrence and intensity of *E. aerophilus* in recent years in southeaster areas of the Iberian Peninsula, compared to the study by Martínez-Carrasco et al. (2007). This suggests a higher risk of *E. aerophilus* infection in fox populations. For this reason, it is advisable to continue monitoring the epidemiological dynamics of *E. aerophilus* and implement measures to prevent the nematode spread, especially in areas where humans, domestic and wild host species interact.

5. Conclusions

The red fox is a wild host that participates in the maintenance of the sylvatic cycle of *E. aerophilus* in semi-arid Mediterranean areas, which should be considered to interpretate the epidemiology of this shared nematode at the domestic-wild-human interface. Although our study is based on a limited number of foxes, it provides novel insights into how environmental factors influence *E. aerophilus* distribution. This information should be complemented in the future by a larger sample size of hosts, including dogs. Our findings indicate that occurrence and parasite intensity are higher in forested areas, offering valuable insights for guiding future preventive measures. Consequently, foxes should be a key focus of interest for epidemiological studies carried out in rural and peri-urban areas.

CRediT authorship contribution statement

I. Arcenillas-Hernández: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **M. Català-Barrasetas:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **P. Pérez-Cutillas:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **M.R. Ruiz de Ybáñez:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **C. Martínez-Carrasco:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

None.

Acknowledgments

This work was supported by the Autonomous Community of the Region of Murcia (Spain), through the Regional Programme for the Promotion of Research (Action Plan 2019) of the Seneca Foundation, Science and Technology Agency of the Region of Murcia [grant number 20952/PI/18].

References

Aftandelians, R., Raafat, F., Taffazoli, M., Beaver, P.C., 1977. Pulmonary capillariasis in a child in Iran. J. Trop. Med. Hyg. 26 (1), 64–71.

Alcaraz, F., Barreña, J.A., Clemente, M., González, A.J., López, J., Rivera, D., Ríos, S., 2008. Manual de Interpretación de los Hábitats Naturales y Seminaturales de la Región de Murcia. In: Tomo I: Hábitats y Sistemas de Hábitats. Dirección General del Medio Natural Consejería de Desarrollo Sostenible y Ordenación del Territorio, Región de Murcia.

Al-Sabi, M.N., Halasa, T., Kapel, C.M., 2014. Infections with cardiopulmonary and intestinal helminths and sarcoptic mange in red foxes from two different localities in Denmark. Acta Parasitol. 59 (1), 98–107.

Anderson, R.C., 2000. Nematode parasites of vertebrates. In: Their Development and Transmission 2nd Ed. CABI Publishing.

Keys to the nematode parasites of vertebrates: Archival volume. In: Anderson, R.C., Chabaud, A.G., Willmott, S. (Eds.), 2009. CABI, 463 Pages, https://doi.org/10.1079/9781845935726.0000.

Arcenillas-Hernández, I., de Ybáñez, M.R., Tizzani, P., Pérez-Cutillas, P., Martínez-Carrasco, C., 2022. *Pearsonema plica* in red foxes (*Vulpes vulpes*) from semi-arid areas of the Iberian Peninsula. Int. J. Parasitol. Parasites Wildl. 19, 78–83.

Arcenillas-Hernández, I., Ruiz de Ybáñez, M.R., Martínez-Carrasco, C., 2023. What is the sensitivity and exactness of post-mortem diagnostic method for cardiopulmonary nematodes in wild carnivores? Towards the gold standard. Vet. Res. Commun. 47 (3), 1369–1378.

Arcenillas-Hernández, I., Ruiz de Ybáñez, M.R., Tizzani, P., Pérez-Cutillas, P., Martínez-Carrasco, C., 2024. Influence of environmental factors on the occurrence of gastrointestinal and cardiopulmonary nematodes in the red fox in the semi-arid Mediterranean areas of the Iberian Peninsula. Res. Vet. Sci. 171, 105199.

ASTER GDEM, 2018. NASA/METI/AIST/Japan Spacesystems, and U.S./Japan ASTER Science Team. ASTER Global Digital Elevation Model V003. 2018, distributed by NASA EOSDIS Land Processes DAAC. https://doi.org/10.5067/ASTER/ASTGTM.003.

Barbosa, A.M., Segovia, J.M., Vargas, J.M., Torres, J., Real, R., Miquel, J., 2005. Predictors of red fox (*Vulpes vulpes*). Helminth parasite diversity in the provinces of Spain. Wildl. Biol. Pract. 1 (1), 3–14.

Bružinskaitė-Schmidhalter, R., Šarkūnas, M., Malakauskas, A., Mathis, A., Torgerson, P. R., Deplazes, P., 2011. Helminths of red foxes (*Vulpes vulpes*) and raccoon dogs (*Nyctereutes procyonoides*) in Lithuania. Parasitology 139 (1), 120–127.

Bush, A.O., Lafferty, D., Lotz, J.M., Shostak, A.W., 1997. Parasitology meets ecology on own terms: Margolis et al. revisited. J. Parasitol. 83 (4), 575–583.

Ćabrilo, O.B., Simin, V., Miljević, M., Ćabrilo, B., Mijatović, D., Lalošević, D., 2018. Respiratory and cardiopulmonary nematode species of foxes and jackals in Serbia. Helminthologia 55 (3), 213–221.

Contesse, P., Hegglin, D., Gloor, S., Bontadina, F., Deplazes, P., 2004. The diet of urban foxes (*Vulpes vulpes*) and the availability of anthropogenic food in the city of Zurich, Switzerland. Mamm. Biol. 69, 81–95.

Davidson, R.K., Gjerde, B., Vikøren, T., Lillehaug, A., Handeland, K., 2006. Prevalence of *trichinella* larvae and extra-intestinal nematodes in Norwegian red foxes (*Vulpes vulpes*). Vet. Parasitol. 136 (3–4), 307–316.

Deak, G., Gherman, C.M., Ionica, A.M., Péter, A., Sándor, A.D., Mihalca, A.D., 2020. Biotic and abiotic factors influencing the prevalence, intensity and distribution of *Eucoleus aerophilus* and *Crenosoma vulpis* in red foxes, *Vulpes vulpes* from Romania. Int. J. Parasitol. Parasites Wildl. 12, 121–125.

Decristophoris, P.Md., von Hardenberg, A., McElligott, A.G., 2007. Testosterone is positively related to the output of nematode eggs in male Alpine ibex (*Capra ibex*) faeces. Evol. Ecol. Res. 9, 1277–1292.

Di Cesare, A., Otranto, D., Latrofa, M.S., Veronesi, F., Perrucci, S., Lalosevic, D., Gherman, C.M., Traversa, D., 2014. Genetic variability of *Eucoleus aerophilus* from domestic and wild hosts. Res. Vet. Sci. 96 (3), 512–515.

Díaz-Ruiz, F., Delibes-Mateos, M., García-Moreno, L., López-Martín, J.M., Ferreira, C., Ferreras, P., 2013. Bioeographical patterns in the diet of an opportunistic predator: the red fox (*Vulpes vulpes*) in the Iberian Peninsula. Mammal Rev. 43, 59–70.

Eira, C., Vingada, J., Torres, J., Miquel, J., 2006. The helminth community of the red fox, *vulpes vulpes*, in Dunas de Mira (Portugal) and its effect on host condition. Wildl. Biol. Pract. 2 (1), 26–36.

Folstad, I., Karter, J.A., 1992. Parasites, bright males, and the immunocompetence handicap. Am. Nat. 139, 603–622.

Franssen, F., Nijsse, R., Mulder, J., Cremers, H., Dam, C., Takumi, K., Van Der Giessen, J., 2014. Increase in number of helminth species from Dutch red foxes over a 35-year period. Parasit. Vectors 7, 166.

García, I., Robledano, F., Esteve, M.A., 2009. Abundancias y densidades relativas de zorro *Vulpes vulpes* (Linnaeus, 1758) en un humedal del sudeste ibérico: implicaciones para la conservación de sus poblaciones. An. Biol. 31, 42–48.

Gavrilović, P., Dobrosavljević, I., Vasković, N., Todorović, I., Živulj, A., Kureljušić, B., Pavlović, I., 2019. Cardiopulmonary parasitic nematodes of the red fox (*Vulpes vulpes*) in Serbia. Acta Vet. Hung. 67 (1), 60–69.

Gloor, S., Bontadina, F., Hegglin, D., Deplazes, P., Breitenmoser, U., 2001. The rise of urban fox populations in Switzerland. Mamm. Biol. 66, 155–164.

Gortázar, C., 2007. *Vulpes vulpes* (Linnaeus, 1758). In: Palomo, L.J., Gisbert, J., Blanco, J. C. (Eds.), Atlas y Libro Rojo de los Mamíferos Terrestres de España. Dirección General para la Biodiversidad -SECEM-SECEMU, Madrid, pp. 277–279.

Gourbière, S., Morand, S., Waxman, D., 2015. Fundamental factors determining the nature of parasite aggregation in hosts. PLoS One 10 (2), e0116893.

Hodžić, A., Alić, A., Klebić, I., Kadrić, M., Brianti, E., Duscher, G.G., 2016. Red fox (*Vulpes vulpes*) as a potential reservoir host of cardiorespiratory parasites in Bosnia and Herzegovina. Vet. Parasitol. 223, 63–70.

INE (Instituto Nacional de Estadística), 2020. Indicadores para secciones censales y cartografía digitalizada.

Karamon, J., Dąbrowska, J., Kochanowski, M., Samorek-Pieróg, M., Sroka, J., Różycki, M., Bilska-Zając, E., Zdybel, J., Cencek, T., 2018. Prevalence of intestinal helminths of red foxes (*Vulpes vulpes*) in Central Europe (Poland): a significant zoonotic threat. Parasit. Vectors 11 (1), 436.

Lalošević, D., Lalošević, V., Klem, I., Stanojev-Jovanović, D., Pozio, E., 2008. Pulmonary capillariasis miming bronchial carcinoma. ASTMH 78 (1), 14–16.

Lalošević, V., Lalošević, D., Čapo, I., Simin, V., Galfi, A., Traversa, D., 2013. High infection rate of zoonotic *Eucoleus aerophilus* infection in foxes from Serbia. Parasite 20, 3.

Lindenfors, P., Nunn, C.L., Jones, K.E., Cunningham, A.A., Sechrest, W., Gittleman, J.L., 2007. Parasites species richness in carnivores: effects of host body mass, latitude, geographical range and population density. Glob. Ecol. Biogeogr. 16, 496–509.

Magi, M., Macchioni, F., Dell'omodarme, M., Prati, M.C., Calderini, P., Gabrielli, S., Iori, A., Cancrini, G., 2009. Endoparasites of red fox (*Vulpes vulpes*) in Central Italy. J. Wildl. Dis. 45 (3), 881–885.

Magi, M., Guardone, L., Prati, M.C., Mignone, W., Macchioni, F., 2015. Extraintestinal nematodes of the red fox *Vulpes vulpes* in north-West Italy. J. Helminthol. 89 (4), 506–511.

Mañas, S., Ferrer, D., Castellà, J., Maria López-Martín, J., 2005. Cardiopulmonary helminth parasites of red foxes (*Vulpes vulpes*) in Catalonia, northeastern Spain. Vet. J. 169 (1), 118–120.

Manfredi, M.T., Giacomett, I.A., Franquelli, C., Piccolo, G., 2003. Studio della popolazione elmintica in volpi (*Vulpes vulpes*) del Trentino Alto-Adige. J. Mt. Ecol. 7, 261–263.

Margolis, L., Esch, G.W., Holmes, J.C., Kuris, A.M., Schad, A.G., 1982. The use of ecological terms in parasitology (report of an ad hoc committee of the American Society of Parasitologists). J. Parasitol. 68 (1), 131–133.

Martínez-Carrasco, C., Ruiz de Ybañez, M.R., Sagarminaga, J.L., Garijo, M.M., Moreno, F., Acosta, I., Hernández, S., Alonso, F.D., 2007. Parasites of the red fox (*Vulpes vulpes* Linnaeus, 1758) in Murcia, Southeast Spain. Rev. Med. Vet. 158 (7), 331–335.

Martínez-Rondán, F.J., Ruiz de Ybáñez, M.R., López-Beceiro, A.M., Fidalgo, L.E., Berriatua, E., Lahat, L., Sacristán, I., Oleaga, A., Martínez-Carrasco, C., 2019. Cardiopulmonary nematode infections in wild canids: does the key lie on host-prey-parasite evolution? Res. Vet. Sci. 126, 51–58.

Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO), 2024. Mapa Forestal de España (MFE). Banco de Datos de la Naturaleza. https://biodatos.miteco.es/.

Miró, J., Estrela, M.J., Caselles, V., Gómez, I., 2018. Spatial and temporal rainfall changes in the Júcar and Segura basins (1955–2016): fine-scale trends. Int. J. Climatol. 38 (13), 4699–4722.

Morgan, E.R., Tomlinson, A., Hunter, S., Nichols, T., Roberts, E., Fox, M.T., Taylor, M.A., 2008. *Angiostrongylus vasorum* and *Eucoleus aerophilus* in foxes (*Vulpes vulpes*) in Great Britain. Vet. Parasitol. 154 (1–2), 48–57.

Nevárez, A., López, A., Conboy, G., Ireland, W., Sims, D., 2005. Distribution of *Crenosoma vulpis* and *Eucoleus aerophilus* in the lung of free-ranging red foxes (*Vulpes vulpes*). J. Vet. Diagn. Invest. 17 (5), 486–489.

Ninyerola, M., Pons, X., Roure, J.M., 2005. Atlas Climático Digital de la Península Ibérica. Metodología y Aplicaciones en Bioclimatología y Geobotánica. Universidad Autónoma de Barcelona, Bellaterra. Available. http://www.opengis.uab.es/wms/iberia/index.htm.

Nonnis, F., Tamponi, C., Tosciri, G., Manconi, M., Pudda, F., Cabras, P., Dessì, G., Scala, A., Varcasia, A., 2023. Cardio-pulmonary nematodes of the red fox (*Vulpes vulpes*) of Sardinia, Italy. Parasitol. Res. 122 (7), 1685–1688.

Otranto, D., Deplazes, P., 2019. Zoonotic nematodes of wild carnivores. Int. J. Parasitol. Parasites Wildl. 9, 370–383.

Perrucci, S., Di Cesare, A., Fichi, G., 2014. In vitro development of *Eucoleus böhmi* eggs in different environmental conditions. Parasitol. Res. 113 (7), 2687–2691.

Polotzek, M., van der Neut, F., Keiser, P., Lindhorst, Z.T.L., Kühling, A.K., Hering-Hagenbeck, S., Fuehrer, H.P., Ebmer, D., 2025. *Eucoleus aerophilus* (syn. *Capillaria aerophila*) infection in zoo-housed arctic foxes (*Vulpes lagopus*). Acta Parasitol. 70 (2), 69.

Poulin, R., 2007. Are there general laws in parasite ecology? Parasitology 134 (6), 763–776.

QGIS Development Team, 2024. QGIS Geographic Information System. Open-Source Geospatial Foundation Project. Retrieved from. http://qgis.osgeo.org.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rajković-Janje, R., Marinculić, A., Bosnić, S., Benić, M., Vinković, B., Mihaljević, Ž., 2002. Prevalence and seasonal distribution of helminth parasites in red foxes (*Vulpes vulpes*) from the Zagreb County (Croatia). Z. Jagdwissensch. 48, 151–160.

Riney, T., 1955. Evaluating condition of free-ranging red deer (*Cervus elaphus*), with special reference to New Zealand. N. Z. J. Sci. Technol. 36, 430–463.

Roberts, M.L., Buchanan, K.L., Evans, M.R., 2004. Testing the immunocompetence handicap hypothesis: a review of the evidence. Anim. Behav. 68 (2), 227–239.

Saeed, I., Maddox-Hyttel, C., Monrad, J., Kapel, C.M., 2006. Helminths of red foxes (*Vulpes vulpes*) in Denmark. Vet. Parasitol. 139 (1–3), 168–179.

Sáenz de Buruaga, M., Lucio, A.J., Purroy, F.J., 1991. Reconocimiento de sexo y edad de especies cinegéticas. Gobierno Vasco, Vitoria.

Samorek-Pieróg, M., Cencek, T., Łabuć, E., Pac-Sosińska, M., Pieróg, M., Korpysa-Dzirba, W., Bełcik, A., Bilska-Zając, E., Karamon, J., 2023. Occurrence of *Eucoleus aerophilus* in wild and domestic animals: a systematic review and meta-analysis. Parasit. Vectors 16 (1), 245.

Samorek-Pieróg, M., Cencek, T., Bilska-Zając, E., Korpysa-Dzirba, W., Bełcik, A., Sroka, J., Lass, A., Brzana, A., Karamon, J., 2024. Prevalence and genetic diversity of the lung nematode *Eucoleus aerophilus* in red foxes (*Vulpes vulpes*) in Central Europe (Poland) assessed by PCR and flotation. Sci. Rep. 14 (1), 24030.

Schug, K., Krämer, F., Schaper, R., Hirzmann, J., Failing, K., Hermosilla, C., Taubert, A., 2018. Prevalence survey on lungworm (*Angiostrongylus vasorum*, *Crenosoma vulpis*, *Eucoleus aerophilus*) infections of wild red foxes (*Vulpes vulpes*) in Central Germany. Parasit. Vectors 11 (1), 85.

Segovia, J.M., Torres, J., Miquel, J., 2004. Helminth parasites of the red fox (*Vulpes vulpes* L., 1758) in the Iberian Peninsula: an ecological study. Acta Parasitol. 49 (1), 67–79.

Singh, J., Schädler, M., Demetrio, W., Brown, G.G., Eisenhauer, N., 2019. Climate change effects on earthworms – a review. Soil Organ. 91 (3), 113–137.

Soe, E., Davison, J., Süld, K., Valdmann, H., Laurimaa, L., Saarma, U., 2017. Europe-wide biogeographical patterns in the diet of an ecologically and epidemiologically important mesopredator, the red fox (*Vulpes vulpes*): a quantitative review. Mammal Rev. 47, 198–211.

Sréter, T., Széll, Z., Marucci, G., Pozio, E., Varga, I., 2003. Extraintestinal nematode infections of red foxes (*Vulpes vulpes*) in Hungary. Vet. Parasitol. 115 (4), 329–334.

Tamaru, M., Sakaguchi, S., Souzu, Y., Murata, K., Yunus, M., Rosyadi, I., Sato, H., 2025. Integrated taxonomic approaches to gastrointestinal and urinary capillariid nematodes from wild and domestic mammals. Pathogens 14 (5), 455.

Tolnai, Z., Széll, Z., Sréter, T., 2015. Environmental determinants of the spatial distribution of *Angiostrongylus vasorum*, *Crenosoma vulpis* and *Eucoleus aerophilus* in Hungary. Vet. Parasitol. 207, 355–358.

Traversa, D., Di Cesare, A., Milillo, P., Iorio, R., Otranto, D., 2009. Infection by *Eucoleus aerophilus* in dogs and cats: is another extra-intestinal parasitic nematode of pets emerging in Italy? Res. Vet. Sci. 87 (2), 270–272.

Traversa, D., Di Cesare, A., Conboy, G., 2010. Canine and feline cardiopulmonary parasitic nematodes in Europe: emerging and underestimated. Parasit. Vectors 3, 62.

Traversa, D., Di Cesare, A., Lia, R.P., Castagna, G., Meloni, S., Heine, J., Strube, K., Milillo, P., Otranto, D., Meckes, O., Schaper, R., 2011. New insights into morphological and biological features of *Capillaria aerophila* (Trichocephalida, Trichuridae). Parasitol. Res. 109 (1), S97–S104.

Twardosz, R., Walanus, A., Guzik, I., 2021. Warming in Europe: recent trends in annual and seasonal temperatures. Pure Appl. Geophys. 178 (10), 4021–4032.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics with S, 4th ed. Springer, New York.

Willingham, A.L., Ockens, N.W., Kapel, C.M., Monrad, J., 1996. A helminthological survey of wild red foxes (*Vulpes vulpes*) from the metropolitan area of Copenhagen. J. Helminthol. 70 (3), 259–263.

Winstanley, R.K., Saunders, G., Buttemer, W.A., 1998. Indices for predicting total body fat in red foxes from Australia. J. Wildl. Manag. 62 (4), 1307–1312.

Wolfe, A., Hogan, S., Maguire, D., Fitzpatrick, C., Vaughan, L., Wall, D., Hayden, T.J., Mulcahy, G., 2001. Red foxes (*Vulpes vulpes*) in Ireland as hosts for parasites of potential zoonotic and veterinary significance. Vet. Rec. 149 (25), 759–763.